THE INTERACTION BETWEEN WATER TURBIDITY AND VISUAL SENSORY SYSTEMS AND ITS IMPACT ON FRESHWATER FISHES

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Abstract

An aquatic ecosystem's sensory environment has a profound influence on multiple aspects of the life cycles of its resident species, including mating cues, predation, and sensory systems. This thesis consists of laboratory studies and a meta-analysis that examines how changing aquatic sensory information, by reducing visual information through turbidity manipulation, can impact fish species. The laboratory studies focused on the consequences of changes in turbidity on the predator-prey interactions of two native Newfoundland fish species (three-spined stickleback prey, *Gasterosteus aculeatu*s, and predatory brook trout, *Salvelinus fontinalis*). The results illustrated that reducing visibility may give a prey species a sensory advantage over a predator, potentially influencing their dynamics. In order to understand the impacts of turbidity on a larger scale, I undertook a meta-analysis on fluctuations in fish communities in relation to shifts in turbidity due to reservoir creation. The analyses indicated that differential changes in turbidity influence the biodiversity and evenness of the visual subset of the fish community. Understanding how changes to the sensory environment can influence aquatic ecosystems is crucial when providing predictions for the potential outcomes of proposed anthropogenic activities altering water turbidity.

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Chapter 1 : General Introduction

Anthropogenic effects impact aquatic environments (Mills et al. 1993; Utne-Palm 2002; Tuomainen and Candolin 2011; Ferrari et al. 2014), and these impacts affect the performances of aquatic species. These species have evolved sensory systems that can give them a competitive edge within their habitat's biological, physical, and chemical characteristics (Endler 1992). However, a sudden, rapid change in an environmental factor, such as turbidity, may result in previously beneficial phenotypes no longer conferring the same selective advantages (Vitousek 1994; Dudgeon et al. 2006). This shift in the sensory environment can have far-reaching impacts on aquatic communities by altering the behaviours of species (Robinson and Tonn 1989; Tonn et al. 1990; Rahel and Hubert 1991) and changing community composition.

Fish species detect their predators and prey through electrical, auditory (including pressure), chemical, and visual cues (Abrahams 2005), with species frequently engaging more than one sensory system at a time. Species invest energy in different sensory systems based upon their environmental conditions, and their morphology reflects these investments (Kotrschal et al. 1998; Niven and Laughlin 2008). Variations in the size of the brain's sensory structures relate to evolutionary adaptations of the species to past habitat conditions leading to the evolution of characteristic brain morphology (Kotrschal et al. 1998; Dieterman and Galat 2005). A difference in the size of the optic lobes, olfactory bulbs, telencephalon, and cerebella (Sylvester et al. 2010) reflects the primary sensory systems for a species. However, the development of one part of the brain does not necessarily mean a deficiency in other parts of the brain (Huber et al. 1997). Rather,

brain development can indicate which sensory systems a species uses most. The exterior morphology can be reflected in the size of the eye, including the density and size of photoreceptors (Pankhurst 1989; Fishelson et al. 2004), as well as additional structures such as exterior taste buds located on the fish body, fins, barbells, lip papillae (Bardach et al. 1967; Kasumyan and Doving 2003), or specialized electric organs (von der Emde 2006; von der Emde and Fetz 2007). In many aquatic ecosystems, the majority of fishes primarily feed visually (Guthrie and Muntz 1992; Domenici 2002; De Robertis et al. 2003; Jönsson et al. 2013), requiring well-developed optic lobes (Kotrschal et al. 1998; Huber et al. 1997), and eyes (Pankhurst 1989; Fishelson et al. 2004). Conditions that alter the physical condition of the environment and significantly influence the visibility can impact many species (Gregory and Northcote 1993; Utne 1997; Utne-Palm 2002; Meager et al. 2006).

Visibility depends on a fish's ability to detect the contrast between the stimuli of interest and the background (Utne-Palm 1999). The amount of light in the environment, the species' visual capabilities, and the scattering of light between the viewer and the object all affect this contrast (Aksnes and Giske 1993; Utne-Palm 2002). Turbidity, measured in Nephelometric Turbidity Units (NTU) as the amount of scattering of light caused by suspended particulate matter (Duchrow and Everhart 1971; Gray et al. 2014), reduces the contrast between an object and its background. These suspended particles, whether algae, clay, or humic matter (Ranåker et al. 2012), scatter light (Benfield and Minello 1996; Jönsson et al. 2013), thereby decreasing image quality, object visibility, and detectability, especially at greater distances (Utne-Palm 2002; Jönsson et al. 2013).

Changes in turbidity can, by influencing their behaviours, differentially affect predator and prey species, thereby shifting predator-prey relationships (Miner and Stein 1996; Meager et al. 2006). Behavioural responses to their ecosystem have evolved over time (Dill 1987; Tuomainen and Candolin 2011) and the evolved behaviour of both predator and prey species influence predator-prey responses (Sih et al. 2010). Changes in the behavioural dynamics of predator-prey relationships could impact the foraging abilities of the predator (Jönsson et al. 2013) and alter the relative concentrations of predator and prey populations.

Predator-prey interactions offer a measure of turbidity changes can alter populations of aquatic species and play a key role in predicting ecosystem responses to environmental change (Jacobsen et al. 2014). Turbidity impacts reaction distances (i.e., the distance at which an animal reacts to an object in its environment) and these distances provide a measure of the range of a species' detection capability (Aksnes and Giske 1993; Utne-Palm 1999). Increased turbidity decreases the range of visibility (De Robertis et al. 2003; Chiu and Abrahams 2010) of both predator and prey species (Vogel and Beauchamp 1999; Utne-Palm 2002; Meager et al. 2006; Jönsson et al. 2013). With increased turbidity, visual predators may no longer detect their prey at further distances (Meager et al. 2006), with consequent negative impacts on their effectiveness as visual predators (De Robertis et al. 2003; Radke and Gaupisch 2005; Chiu and Abrahams 2010). Increased turbidity can also impact prey species by reducing their ability to detect a predator, thereby compromising the preys' antipredator behaviour and leading them to engage in riskier activities (Utne-Palm 2002) if they do not detect other sensory cues

related to predator presence (Hartman and Abrahams 2000). While changes in turbidity that impact predator-prey dynamics can occur naturally, anthropogenic activities can also alter turbidity (Scheffer et al. 2001).

Anthropogenic effects that increase turbidity can include human-induced eutrophication through point sources (e.g., discharge points from sewage systems and industrial plants; de Jonge et al. 2002), as well as diffuse sources (e.g., run-off from agriculture; de Jonge et al. 2002, and areas of deforestation; Gray et al. 2011). Sediment loading caused by mining, urban development, construction (Donohue and Molinos 2009), and highly trafficked roads (Trombulak and Frissel 2000) also causes anthropogenic turbidity changes. The creation of dams and their associated reservoirs is a common anthropogenic occurrence that combines multiple adverse conditions that impact aquatic ecosystems. These impacts include increases in temperature, changes in methylmercury levels, changes in sedimentation, decreases in dissolved oxygen, and changes in turbidity (Rosenberg et al. 1997). Given the global nature of this type of anthropogenic impact (Dynesius and Nilsson 1994), such changes can impact the survival of many aquatic species that depend upon the effectiveness of sensory systems for vital functions such as finding prey, avoiding predation, and selecting mates and habitats (Douglas et al. 1994). Decreasing one species' sensory system effectiveness can also create a new niche that another species can exploit by utilizing a more efficient suite of sensory systems (Douglas et al. 1994).

The repercussions of changing turbidity on fish species define this thesis' central and unifying concept, which explores both the small-scale (interactions within a habitat) and large-scale (changes in fish community composition) ramifications. The study investigates the consequences of changes to the sensory environment within a habitat and the corresponding impacts on fish species. Chapter 2 examines the impact of turbidity on sensory advantages within a laboratory setting. This chapter describes the changes in the abilities of two native Newfoundland species, brook trout (*Salvelinus fontinalis*) and three-spined stickleback (*Gasterosteus aculeatus*) to detect visual stimuli, within a biologically relevant turbidity range. The changes in detection could create a turbidity range where one species could gain an advantage over the other. Chapter 3 broadens understanding of the consequences of turbidity with a meta-analysis examining how changes in turbidity from the impoundment of a body of water can impact the composition of the fish communities. The meta-analysis examines changes in species composition based on the primary sensory modalities of species in the unaltered and altered habitats, overall impacts on biodiversity, species richness, and evenness, and how proportions of visual and non-visual species fluctuate. By examining the repercussions of turbidity from both of these perspectives, I hope to highlight the scale of impacts that a change to the sensory environment can create.

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Co-authorship Statement:

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Chapter 2 : Who benefits when the environment changes? The impact of increasing turbidity on predator-prey dynamics of two fish species

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Abstract

Changes to the sensory environment, through an increase in turbidity, can alter the information to, and influence the decisions made by, fish species. Many species of fish rely on vision as their primary sense to detect prey and avoid predators; consequently, changes in turbidity may impact their rates of detection, thereby influencing predator-prey dynamics. In order to determine if a species in a predator-prey relationship may gain a relative advantage from increasing turbidity, I used video playback analysis to study the rates of detection of a predator (brook trout, *Salvelinus fontinalis)* and prey (three-spined stickleback, *Gasterosteus aculeatus)* to a visual stimulus under increasing turbidity conditions (0 – 20 Nephelometric Turbidity Unit (NTU)). The individual was placed in the center of an octagonal aquarium with eight video monitors placed against its sides. Every 30 seconds, a clip showing the other species approaching was shown, and whether the subject reacted to the stimulus was recorded. My experiments demonstrated that increased turbidity significantly affected the detection rates of both species. The two species differed significantly in rates of detection within the 0-5 NTU range, with higher rates of detection in three-spined sticklebacks than in brook trout. This turbidity range may define a microhabitat refuge for stickleback species that decreases the success rate of the predator, thus altering predator-prey dynamics.

KEYWORDS: turbidity, predator-prey, anthropogenic, sensory systems, detection, brook trout, three-spined stickleback

Introduction:

Predator-prey interactions occur within all ecosystems, including aquatic ecosystems, where they influence patterns of energy flow (Abrahams and Kattenfeld 1997) and play a vital structuring role (Jacobsen et al. 2014). Environmental conditions influence the behaviours of both predator and prey (e.g. Robinson and Tonn 1989; Tonn et al. 1990; Rahel and Hubert 1991). A change in one variable may impact the predator-prey relationship and create a multi-level trophic cascade, affecting the ecosystem as a whole. To understand how a change to the physical environment may alter an ecosystem requires evaluating the impact of physical changes on predator-prey relationships. Within this relationship, predators influence the ecosystem through direct consumption, strongly regulating prey species (Carpenter et al. 1985; Jönsson et al. 2013), as well as impacting lower trophic levels by influencing prey species' behaviour (Carpenter et al. 1985; Dill 1987; Christensen and Persson 1993; Jacobsen et al. 2014). Antipredator behaviours including strategic choice of habitat, feeding areas, feeding time of day, and schooling are influenced by the structural complexity of the environment (Christensen and Persson 1993) and the ability of prey species to detect predator presence (Miner and Stein 1996; Jacobsen et al. 2014). Changes in environmental conditions, such as those that impact visibility, may increase the probability that a prey species does not detect a predator, thus potentially altering antipredator behaviour. Examples of such changes include the choice of feeding areas of bluegill sunfish (*Lepomis macrochirus,* Miner and Stein 1996) and fathead minnows (*Pimephales promelas*, Abrahams and Kattenfeld 1997), and changes in schooling behaviour of roach (*Rutilus rutilus*, Jacobsen et al. 2014). These modifications

can influence prey survival if the predator continues to detect prey under the same conditions, and the prey no longer exhibits the antipredator behaviours to avoid such detection.

Reaction distance (i.e., the distance at which an animal reacts to an object in its environment) provides a measure of the visual range of a species' detection capability (Aksnes and Giske 1993; Utne-Palm 1999), which influences whether prey can escape or are consumed and if predators detect their prey. Changes to the environment may differentially affect the detection abilities of the species, potentially shifting rates of an encounter between predator and prey (Miner and Stein 1996; Meager et al. 2006). The issue of advantage is based upon the probability that an encounter results in prey capture (Lima and Dill 1990). If a prey species can detect the predator first, they can then gain an advantage by decreasing the probability that the encounter leads to capture, through antipredator behaviours to avoid detection or aid escape. However, if a predator detects the prey first, the probability of capture increases and the predator gains the advantage and may consume the prey. Reaction distance is a crucial element of predator-prey relationships, as in many aquatic ecosystems, the majority of fishes are primarily visual (Guthrie and Muntz 1992; Domenici 2002; De Robertis et al. 2003; Jönsson et al. 2013). Consequently, a change in visibility in an aquatic ecosystem can cause far-reaching effects.

The range of a species reaction distance depends upon the visual ability of the fish and on the size and contrast of its target (Giske et al. 1994), as well as the physical

conditions of the aquatic environment (e.g. light level and turbidity level, Utne-Palm 1999). Physical conditions that influence visibility can significantly impact species that depend heavily on vision (Gregory and Northcote 1993; Utne 1997; Utne-Palm 2002; Meager et al. 2006). One such physical condition is turbidity, which is an indicator of the amount of scattering of light caused by suspended particulate matter (Duchrow and Everhart 1971; Gray et al. 2014). To measure the turbidity of collected water samples, researchers commonly use a turbidimeter, which measures the amount of light transmitted in Nephelometric Turbidity Units (NTUs) (Barrett et al. 1992; Gregory and Northcote 1993; Zamor and Grossman 2007; Gray et al. 2014) or, historically, in Jackson Turbidity Units (JTU) (Vinyard and O'Brien 1976). However, other researchers have used a spectrophotometer, which measures the absorbance of light in m^{-1}, to measure turbidity (Utne 1997; Meager et al. 2006). Although specific measurement techniques differ, increased turbidity typically results in a log-linear decline in reaction distance (a proxy for visual abilities) for many species (e.g. bluegill, Vinyard and O'Brian 1976; rainbow trout (*Oncorhynchus myskiss,* Barrett et al. 1992); juvenile Chinook salmon (*Oncorhynchus tshawytscha*, Gregory and Northcote 1993); and the two-spotted goby (*Gobiusculus flavescens,* Utne 1997). A decrease in reaction distance, resulting from decreasing visual information associated with changing environmental conditions, can impact the performance of a species' detection, attack, and escape abilities (Ranåker et al. 2012).

Visibility depends on the ability of the fish to detect the contrast between the stimuli of interest and the background (Utne-Palm 1999). The amount of light in the

environment, the visual capabilities of the species, and the scattering of light between the viewer and the object all affect this contrast (Aksnes and Giske 1993; Utne-Palm 2002). Increased particle concentrations in the water column increase light scattering (Aksnes and Giske 1993; Utne-Palm 2002), and such increases in turbidity can impact the sensory environment by impairing vision and the reaction distance of aquatic species. Anthropogenic impacts such as human-induced eutrophication (Scheffer et al. 2001; de Jonge et al. 2002; Gray et al. 2011) and sediment loading via mining, urban development, and construction (Donohue and Molinos 2009) can all potentially increase turbidity levels and impact aquatic environmental conditions (Mills et al. 1993; Utne-Palm 2002; Ferrari et al. 2014).

Turbidity scatters light (Benfield and Minello 1996; Jönsson et al. 2013), decreasing image quality, object visibility, and detectability, especially at greater distances (Utne-Palm 2002; Jönsson et al. 2013). An increase in turbidity differentially affects both predator and prey species reaction distances (Vogel and Beauchamp 1999; Utne-Palm 2002; Meager et al. 2006; Jönsson et al. 2013), thereby shifting predator-prey relationships (Miner and Stein 1996; Meager et al. 2006). A reduction in the reaction distance for predators to detect prey can decrease encounter rates (Meager et al. 2006). Increased turbidity reduces detection efficacy and negatively impacts predators that rely mainly on vision (De Robertis et al. 2003; Radke and Gaupisch 2005; Chiu and Abrahams 2010), and this reduction can be advantageous to prey species by making them less vulnerable to predation (De Robertis et al. 2003). Consequently, increased turbidity may benefit some prey species. Studies have demonstrated reduced predation on some

prey species in turbid environments (e.g. bluegill sunfish, Miner and Stein 1996; age-0 Chinook salmon, Gregory and Levings 1998), supporting the "turbidity as cover" hypothesis (Gregory 1993). Prey species may also modify their antipredator behaviours at low visibility, for example, change in the duration and intensity of the antipredator response by juvenile Chinook salmon in turbid conditions (Gregory 1993); change in size-specific habitat choice by bluegill sunfish (Miner and Stein 1996); reduction in the use of dangerous habitats by fathead minnows with increased turbidity (Abrahams and Kattenfeld 1997); change in the use of vegetated habitats by age 0+ year perch (*Perca fluviatilis,* Snickars et al. 2004); and change in the use of vegetated habitats and predation on zooplankton by pike larvae (*Esox lucius*, Lehtiniemi et al. 2005). Decreased ability to detect predator cues can result in prey partaking in riskier activities (Utne-Palm 2002), which can also influence predator-prey relationships.

Beyond the effects of turbidity on antipredator behaviours, various prey species also prefer turbid over clear water environments (Blaber and Blaber 1980; Cyrus and Blaber 1987; Maes et al. 1998; Chiu and Abrahams 2010). Chiu and Abrahams (2010) reported that fathead minnow preferred feeding in turbid water over clearer environments, even in the presence of a predator. They hypothesized that the preference did not result from the prey species' inability to detect the predator, but rather from perceived benefits, such as reduced costs associated with antipredator behaviours that offset the potential risk of predation. They further theorized that these differences in habitat choice arise from the preys' detection abilities and that a change in the probability of detection of a stimulus can demonstrate a change in habitat preference. Several

researchers have hypothesized that species prefer habitats that provide an advantage in their ability to detect other species (Miner and Stein 1996; Chiu and Abrahams 2010; Manning et al. 2013). The negative impact of turbidity on the ability of a visual predator to capture prey species enhances the low-risk nature of a turbid environment. This provides prey species with an advantage in detecting a predator before it detects them and allowing the prey to remain hidden in the environment, as seen in the Chiu and Abrahams (2010) experiment. The dynamics within the predator-prey relationship can change when one species in a predator-prey relationship gains a sensory detection advantage in the changed environment.

My study examined the range of turbidity at which a species can gain a sensory advantage by analyzing the ability of a predator and prey species to detect a visual stimulus. Determining whether a specific range of turbidity confers a detection advantage first requires considering the probability that a species can detect visual stimuli within such a range. This study focuses on the relative impact of increasing turbidity on the detection probabilities of a common predator-prey species pair, brook trout (*Salvelinus fontinalis)* and three-spined sticklebacks (*Gasterosteus aculeatus)*, and investigates how they react to visual stimuli (e.g. prey reacting to a visual stimulus of a predator and vice versa). More specifically, I examined the change in detection rates associated with changing turbidity levels in both species, as well as how the impact of these changes can create an advantage for one species and therefore impact their predator-prey relationship. I hypothesized lower rates of detection as turbidity increases in both the predator and prey species; however, the larger size of the stimuli shown to the stickleback should

result in a higher rate of detection in the prey species than in the predator at the higher turbidity levels.

Methods:

Experimental Animals:

I used brook trout and three-spined stickleback, which are a native predator-prey species pair in Newfoundland. The Ocean Science Center dive team captured 150 three-spined sticklebacks in Long Pond (48.000,-55.917) near St. John's, Newfoundland using minnow traps in December 2014. The dive team also captured a total of 40 brook trout, 10-15 cm in length, in Witless Bay Country Pond (47.326687,-52.915395) in Witless Bay, Newfoundland in May-August 2015 using a hook and line. Both ponds are clear (low turbidity) with similar species composition, including trout and stickleback, and similar suites of predators. Within these ponds, other trout species as well as aerial predators, such as the northern loon (*Gavia immer,* personal communication M. Abrahams), prey on trout and stickleback. Limitations imposed by the dive team's schedule necessitated the capture of the trout and stickleback from two different ponds. Although the two locations may differ slightly in turbidity, turbidity levels at both locations were less than 5 NTU (personal communication M. Abrahams). Therefore, the procurement of fish from two different ponds should have a minimal impact on my findings. The fish were transported to the Ocean Sciences Center, Logy Bay, Newfoundland, in coolers filled with water collected at the source and aerated with air stones. All animals were maintained in 1-m diameter circular flow-through tanks, with trout and stickleback in separate tanks, at ambient water temperatures (8-12 ºC) with a

12-hour photoperiod. The trout and stickleback were initially fed a diet of freeze-dried red shrimp (*Solenocera melantho*) (Sun-Dried Large Red Shrimp, Zoo-Med Laboratories, California, USA) and then were transitioned to a commercial fish pellet (1.0 mm and 0.5 mm, respectively) (Corey Aquafeeds, New Brunswick, Canada).

In order to facilitate individual identification, I marked the brook trout with visible implant elastomer (VIE) tags (Northwest Marine Technology, Inc., Washington, USA). I anesthetized the trout using MS-222, measured their fork length, weighed them, and implanted a single VIE tag on each side of the caudal peduncle using a combination of 5 fluorescent colours (red, orange, yellow, blue, and pink). The sticklebacks were not individually identified because I tested each individual only once, and marking would have been unnecessarily invasive.

Experimental Apparatus:

To create a virtual environment I attached eight LCD computer monitors (1280x 1024) with a refresh rate of 75 Hertz (Hz) (Acer 17", Acer Canada, Ontario, Canada) to each exterior side of an octagonal tank. Within this tank, I could manipulate turbidity levels under identical conditions for both predator (brook trout) and prey (three-spined stickleback) (see Figure 2.1). These LCD screens offer a low-flicker alternative to older computer monitors because the pixels consistently glow with no refresh-rate-related flickering (Fleishman and Endler 2000; Chouinard-Thuly et al. 2017). Because computer monitors do not emit ultraviolet (UV) light, this limits the creation of visual stimuli, given that many fish species can see within the UV spectrum (Douglas and Hawryshyn

1990). Three-spined sticklebacks are sensitive to UV light (Rowe et al. 2004); however, the importance of this sensitivity appears to be limited to mate choice (Rick et al. 2004, 2006). UV vision has minimal effects on other predator-prey behaviours such as foraging efficiency (Modarressie and Bakker 2007) and shoal choice (Hiermes et al. 2015); therefore, this limitation should not significantly impact the ability of stickleback to detect the predator. UV-sensitive vision also commonly occurs within the Salmoninae subfamily (Parkyn and Hawryshyn 2000), but this sensitivity declines rapidly as members of this subfamily age (Bowmaker and Kunz 1987; Hawryshyn et al. 1989). Together with the knowledge that this sensitivity contributes to zooplankton detection (Loew and Wahl 1991; Browman and Hawryshyn 1994; Novales-Flamarique and Hawryshyn 1994) rather than piscivorous diets (Browman and Hawryshyn 1994), the lack of UV should minimally impact the ability of trout to detect stickleback. The photopic spectral sensitivity curves of stickleback (445 nm, 530 nm, 605 nm; Lythgoe 1979) and brook trout (425 nm, 545 nm, and 595 nm; Kobayashi and Ali 1971) resemble curves for humans (430 nm, 530 nm and 560 nm; Solomon and Lennie 2007). Therefore, I presented colour values on the screen within a range that looked as natural as possible to humans. While the colour vision of test fish is not the same as humans, faithful reproduction of colour was not essential for my study, because the colour is not an aspect necessary for the animal to produce a response (D'Eath 1998; Chouinard-Thuly et al. 2017).

For each trial, I held an individual within a circular tank (30 cm diameter) in the middle of a larger octagonal tank (1 m diameter). The inner circular tank contained clear

water, while I adjusted the surrounding water to achieve one of the five turbidity levels, expressed in NTUs, (0, 5, 10, 15, and 20 NTU). I chose this range of turbidity because it spans a broad spectrum where changes between the levels differ visibly (personal observation), it encompasses the natural turbidity conditions of the habitat the species were collected from, and turbidity alterations within this range alter fish behaviour (Barrett et al. 1992; De Robertis et al. 2003; Trebitz et al. 2007; Zamor and Grossman 2007; Gray et al. 2014). The turbidity level remained consistent during the acclimation and trial period (personal observation). I filled the inner tank with clear water in order to observe the behaviours of the study animals.

I manipulated turbidity by adding dry bentonite clay (80-100 g) to a 100-ml beaker containing distilled water, stirring the solution for an hour to create a slurry, and then allowing it to settle for 48 hours. Settling allowed the larger particles of bentonite to precipitate, leaving only the finer particles suspended in solution. I used the remaining fine bentonite solution in the apparatus to create the five levels of turbidity by adding it to the surrounding clear water in the exterior tank 10 ml at a time before stirring the water and letting it settle for 2 minutes. After each addition of the bentonite solution, I measured turbidity using a Hach Laboratory Turbidimeter Model 2100N (Hach Canada, Ontario, Canada), which quantifies the amount of light from a tungsten bulb at an angle of 90+/-30º in NTU. I adjusted turbidity by adding or removing bentonite solution (and adding clear water) to achieve the target turbidity (within one decimal place of the desired NTU). The clear water was brought in from the Marine Institute because tannins from surrounding trees stain the freshwater available at the Ocean Science Center.

Between trials, two air stones placed in the exterior tank maintained the turbidity by resuspending any settled bentonite particles back into the water column.

For the visual stimuli, I recorded six-second clips of (1) a trout swimming toward the camera and (2) a stickleback swimming toward the HD camera (Canon Vixia HF R60). The trout and stickleback filmed for the stimuli were not used during the trials. Given that a fish might react to a change in brightness rather than the stimulus, the stimulus recordings were conducted under identical conditions: a consistent source of light, covering of windows to eliminate changes caused by sunlight and shadows, covering the sides of the aquarium (20”x10”x12”) with a cardboard box to eliminate glare, and positioning the HD camera on a tripod, next to the tank, that was not moved between filming the stimuli to ensure the distance from the tank was consistent. These measures ensured that minimal changes in brightness when a stimulus appeared could occur, greatly reducing the possibility of experimental error. I recorded eight DVDs of identical video footage displaying the interior of a tank with a gravel bottom. I then randomly spliced a fish swimming clip into one of the eight DVDs every 30 seconds for the duration of the video footage, using iMovie software. I reviewed the fish swimming clip to ensure that both the predator and prey videos the fish appeared at their natural size. I used a random number generator to decide which of the eight DVDs to splice in the fish swimming clip at each 30-second interval. Each video had a frame rate of 30 frames per second (fps), the widely used and validated frame rate for fish (Fleishman and Endler 2000; Oliveira et al. 2000; Chouinard-Thuly et al. 2017). This frame rate, as well as the low-flicker LCD screens with refresh rates of 75 HZ, ensured that test subjects

perceived a flicker-free virtual environment with a smooth motion for each stimulus. I randomly assigned each DVD to a monitor at the beginning of each individual trial with all monitors displaying identical video footage of an aquatic environment: an interior of a tank with a gravel bottom. Every 30 seconds, one of the eight monitors would change to display the video clip of a fish swimming towards the camera. For stickleback trials, I displayed the trout clip, whereas, for trout trials, I displayed the stickleback clip. After each six-second clip ended, the monitor reverted to display the default tank with a gravel bottom. Each trial lasted 20 minutes, with a total of 40 iterations of the presentation of the fish stimuli per trial.

Experimental Design, Procedure, and Video Analysis:

I conducted stickleback trials in May 2015 and brook trout trials from June – September 2015. The trout trials were completed later in the year, because I could not procure the license for the procurement of the trout until May 2015, and the trout needed to re-acclimatize to the conditions of the lab after the implantation of the VIE tags. During this acclimatization, I completed the stickleback trials. The brook trout experiments used a repeated measures design, where I presented each brook trout with each of the five turbidity conditions. A repeated measures design was necessary because it was impractical to capture and house sufficient brook trout for each individual to be tested only once (as was done with sticklebacks). This design was also feasible for the brook trout trials because individual brook trout, after the implantation of the VIE tags, were easily identifiable. The sticklebacks were only used once in a completely

randomized design. Sticklebacks were randomly selected from the holding tank and placed into a new tank upon completion of the trial, whereas the brook trout were identified via their tags at the end of each trial and given at least 12 hrs to recover between trials to minimize stress. I selected the sequence of turbidity levels randomly (15, 20, 0, 10, and 5 NTU) and used that sequence for all trials because of logistical issues involving the need to add clear water (not available on-site) each time a turbidity level decreased. I cooled the water in the central experimental tank to 10-12 °C before beginning each 25 minute acclimation period and measured turbidity levels before and after each trial. I discarded results if the turbidity levels changed by more than 20%. The fish were moved between the holding tank and the experimental tank via a bucket filled with clear water and an air stone.

In order to determine whether the fish detected the stimulus, I videotaped the test subject with a digital video camera (located above the tank) and recorded both neutral behaviour (defined as swimming behaviours displayed in the absence of a stimulus) and reactive behaviours responding to the stimuli (see Table 2.1 for a list of behaviours used). For this study, I assumed that reactive behaviours indicate visual detection of that stimulus. This assumption was necessary because a detection that does not elicit any changes in behaviour can not be observed in the video playback and therefore, cannot be quantified within the confines of this study. Reactive behaviours were chosen based upon the review of the two-hour video taken to obtain the stimulus clip and from documented foraging and antipredator behaviours described in peer-reviewed papers. To avoid perception bias I reviewed each of these videos blindly, without knowledge of which

screen was presenting the stimulus, recording each presentation of the stimulus every 30 seconds, as either a reaction (assumed to indicate detection of the stimulus) or no reaction (in this case assumed to indicate no detection of the stimulus, although technically I cannot rule out a detection in the absence of a visible response) based upon the individual presenting a reactive behaviour during the 6-second presentation period. I then re-examined each video to determine if the reactive behaviour occurred at the same time and location as the appearance of the stimulus.

Given the presentation of each clip of the stimulus every 30 seconds, the blind review of the videos may still have an inherent detection bias because I had knowledge of the timing of the stimulus. Background rates of reaction were also measured in order to evaluate the accuracy of the detection probabilities and to counteract a potential bias. To estimate the background rates for the behaviours used for stimulus detection, I re-analyzed each video for the six-seconds prior to the stimulus (40 iterations). Based on the results from the re-analysis of the videos, I concluded that the level of background reactions, behaviours based on table 2.1 (0-3% for both species) was representative of species behaviour in the absence of a stimulus. I then subtracted the number of times that an individual displayed reactive behaviours during these non-stimulus times from the total reactions during the trial and used the resulting number to calculate the proportion of detection of the visual stimulus by dividing the number of times that the individual reacted to the stimulus by the total number of times that the stimulus was shown (n=40).

Data Analysis

All analyses used α set at 0.05. I examined the residuals to test the assumptions of the linear model. All analyses were completed in R version 3.3.3(R Core Team 2013) with the car (Fox and Weisberg 2019), lme4 (Bates et al. 2015), and lsmeans (Lenth 2016) package and visualizations used ggplot2 (Wickham 2016) and multcompView (Graves et al. 2019) packages.

Given some logistical differences in experimental design (see above) between the brook trout (repeated measures) and stickleback (non-repeated measures) experiments, I analyzed the two species separately. The stickleback analysis used a general linear model (LM), with the turbidity level as a fixed factor. The trout analysis used a linear mixed-effects model (LMM), which added individual as a random factor. Both models were analyzed using analysis of variance (ANOVA) to determine the significance of turbidity on the detection of visual stimuli. Although I randomized stimulus presentation order overall, the logistics of water changes in my experimental set-up (see above) necessitated using the same order for all subjects. Therefore, I could not include order as a random factor in the model, as would usually be the case, because the order was confounded with turbidity level. Instead, I plotted the detection rate vs. the order of turbidity trials (Figure 2.2) to test for habituation.

To determine the intraspecific effects of different turbidity levels on the detection of a visual stimulus, I ran posthoc pairwise comparisons using the Tukey method for multiple comparisons, through the “lsmeans” package in R (Lenth 2016) for both the

trout and stickleback models separately. To compare the interspecific response to turbidity, I used a confidence interval (CI) approach (Nakagawa and Cuthill 2007) to compare the contrasts reported from each pairwise comparison. This approach offered a conservative method to compare the results from two different experimental designs. The standard error associated with each contrast was used to calculate the confidence intervals for the contrast between each turbidity level for each species. Non-overlapping CIs can be assumed to have a p-value of <0.05, and therefore represent a comparison between two turbidity levels where the two species significantly differ in their responses (Schenker and Gentleman 2001).

Results:

Stickleback reacted to the stimulus with direct and rapid advances either directly toward or away from the screen on which the stimulus appeared (Table 2.1). Brook trout reacted to the stimulus by turning their head and then orienting their body (Table 2.1). At the higher NTU levels (15-20 NTU), the sticklebacks were more likely to position themselves in the middle of the tank, moving in a small area to monitor their surroundings. However, in the clearer, lower turbidity levels, they spent more time freely swimming within the confines of the experimental apparatus. The trout divided their time equally between sedentary bottom-dwelling and free swimming in the tank, regardless of turbidity.

Turbidity significantly affected detection of visual stimulus in both the stickleback ($F_{4, 70} = 16.97$, $p < 0.001$, Figure 2.3A) and brook trout models ($\chi^2_4 = 283.79$,

n=18, p <0.001, Figure 2.3B). For both brook trout and stickleback, the probability of detecting a visual stimulus decreased as turbidity increased (Figure 2.3).

Post-hoc tests showed significant decreases in stimulus detection for stickleback between 0-10 NTU, 0-15 NTU, 0-20 NTU, 5-15 NTU, 5-20 NTU and 10-20 NTU (Table 2.2, Figure 2.3A). For brook trout, stimulus detection decreased significantly at all turbidity levels relative to 0 NTU (Table 2.2, Figure 2.3B). Differences were also significant between 5-10 NTU, 5-15 NTU, 5-20 NTU and 10-20 (Table 2.2, Figure 2.3 B). A comparison of the two species models showed significant interspecific differences in detection (non-overlapping confidence intervals for response contrasts; Schenker and Gentleman 2001) between 0-5 NTU, 0-20 NTU, 5-15 NTU, 5-20 NTU, 10-15 NTU and 10-20 NTU (Figure 2.4).

Discussion:

This study demonstrated that increased turbidity caused a significant decrease in the ability of brook trout and three-spined stickleback to detect a visual stimulus, with significantly lower detection rates at higher turbidity levels than at 0 NTU for species, except for stickleback between 0-5 NTU. On the one hand, brook trout detection rates dropped off rapidly between 0-5 NTU (Figure 2-3), and the plot of the brook trout results suggests a rapid, exponential decline. Once turbidity reached 20 NTU, none of the brook trout tested displayed any reactions toward the visual stimuli. On the other hand, the plot of the detection rates for the stickleback suggests a more linear decline. Brook trout detection rates between consecutive turbidity treatments differed significantly for 0-5

NTU and 5-10 NTU, but not between the higher consecutive turbidity levels. This pattern could suggest low detection rates after 10 NTU. However, stickleback and trout were not impacted in the same way. Whereas turbidity caused a general decline in the detection of the stimuli for the stickleback, the decreases in detection were not significant until turbidity reached 10 NTU. Although the detection rates between consecutive turbidity treatments (5-10 NTU, 10-15 NTU and 15-20 NTU) were not significant, these rates were all significantly lower than the 0 NTU control. However, sticklebacks were still able to detect the visual stimuli at the highest turbidity of 20 NTU, albeit at relatively low levels.

The interspecific comparison of differences in detection rates suggests a low turbidity range (0-5 NTU) in which stickleback may gain a sensory advantage over brook trout, in that stickleback detected the visual stimulus at a significantly higher rate. A prey species with the ability to detect a predator before the predator detects them gain a valuable opportunity to react first (Cerri 1983). As the sticklebacks have higher detection rates than the trout, at low-moderate levels of turbidity, they should be able to detect and consequently react to the trout first, thereby altering the predator-prey dynamics in favour of the sticklebacks. Previous studies have focused on the sensory impact of turbidity on prey detection of planktivorous predators (i.e. prey detection of the two-spotted goby, Utne-Palm 1999), and piscivorous predators (prey detection of lake trout, Vogel and Beauchamp 1999) by comparing the relative change in reaction distance. A study of how turbidity impacted both parties within the predator-prey relationship (juvenile bluegills and largemouth bass (*Micropterus salmoides),* Miner and Stein 1996) also measured

changes in reaction distance to assess detection probability. I designed my study to use the behaviours associated with reactions in order to measure changes in detection probability, rather than use change in the reaction distance, for both species within the predator-prey relationship. Also, unlike those studies, my experiment excluded information from the other senses and focused solely on the impact of visual information on sensory advantages. While this focus allowed me to determine the sole impact of turbidity on vision in this system, it did not address the impact of turbidity on other senses.

I calculated sensory advantage as the difference in responses to a visual stimulus. However, the detection rates for both species were low, with neither exceeding a detection response of 30% (Figure 2.3). I expected these low detection rates given the nature of the trials, in which I provided a solo individual with visual stimulus only, and they reacted to a stimulus that appeared randomly 360 degrees around them. Because three-spined stickleback shoal, I anticipated a weaker response to the stimulus in a single individual compared to the responses of a larger group, as reported in a study of glowlight tetra (*Hemigrammus erythrozonus*), another shoaling fish, and its increasing detection probability with increasing group size (Godin et al. 1988). The field of view of the predator and prey species may also impact responses to visual stimuli. Binocular vision in brook trout provides improved depth perception (Cronin 2005), but trout also have a smaller field of view compared to a prey species that uses its large field of view to monitor for predators from a wide range of directions (Cronin 2005; Tyrrell and Fernández-Juricic 2015). Using their wide field of view, the prey species could then react

to a stimulus near the edge of its field of vision, which the predator species would not see. Another potential limitation of this study is pseudoreplication, a common statistical problem in playback experiments (Rosenthal 1999; McGregor 2000; Oliveira et al. 2000; Kroodsma et al. 2001). The response to a general phenomenon cannot be measured by the repeated presentation of only one stimulus (McGregor 2000), resulting in an inflated sample size for the hypothesis being tested (McGregor et al. 1992). This issue arises because I only used one video for the visual stimulus (either a predator or prey swimming toward the screen) spliced 40 times every 30 seconds into 8 DVDs. However, my hypothesis did not focus on the recognition of the visual stimulus, but rather on how turbidity impacts a species ability to detect a visual stimulus. Keeping the visual stimulus constant, while varying turbidity, allowed me to attribute any changes in detection to changing turbidity rather than a change in the stimulus. Finally, although transitions from the empty tank to the visual stimulus appeared seamless, it is possible that a sudden, slight change in the overall brightness of the stimulus tank could have affected the subjects' response. To control for this potential effect, future studies could control this by splicing alternate 6-second clips of the empty tank into the other seven monitors whenever a stimulus is presented.

The size, contrast, and behaviour of the stimulus that the fish detects relates to the negative impact of turbidity on detection (Utne-Palm 2002). The increase in suspended particles in the water associated with turbidity scatters light, decreasing perceived difference between an object and its background, therefore decreasing the visibility of an object (Utne-Palm 2002; Jönsson et al. 2013). At higher turbidity levels, larger predators,

such as a brook trout, remain visible even at a distance, in contrast to a smaller prey species, such as sticklebacks, which blend into the background of the turbid environment. This visibility difference relates to the impact of turbidity on an object's perceived visibility, even if the perceiver of the object has larger eyes. Higher detection rates give stickleback a sensory advantage over brook trout at turbidity ranges between 0-5 TU. Given this advantage, stickleback may seek out microhabitats within this range in their natural habitats, which may span a wide range of turbidity (e.g., the difference in turbidity in the middle of a reservoir compared to the river mouth area) (Ajemian et al. 2015). Turbidity gradients allow the creation of suitable microhabitats as a result of multiple factors, such as larger particles settling out downstream, the input of clear water from other tributaries, and the composition of surrounding lakeshores, as seen in the permanent turbidity gradient of <4 NTU to >10 NTU in Lake Temiskaming (Zettler and Carter 1986). Refuge choice and prey behaviour can change with different turbidity levels (Engström-Öst et al. 2009), and previous studies show that various prey species may prefer turbid environments over clear water (Blaber and Blaber 1980; Cyrus and Blaber 1987; Maes et al. 1998; Chiu and Abrahams 2010). These turbid microhabitats alter the dynamics of the predator-prey relationship because the prey species may use turbidity as a cover (Gregory 1993; Aksnes and Utne 1997; Chiu and Abrahams 2010) and gain the ability to detect predators at a further distance than the predator can detect and catch them, as described in a juvenile bluegill detection study (Miner and Stein 1996). These changes in behaviour may result from the lower perceived risk of predation, causing the prey to modify their use of costly antipredator behaviours (higher energy

costs and prevention of investing energy on foraging and reproduction) and invest their energy in other behaviours (reproduction and foraging) (Lima and Dill 1990). Within this range, decreased visual acuity could cause brook trout to shift feeding strategies towards a more energetically taxing approach (Sweka and Hartman 2001a) in order to catch prey with a visual sensory advantage. This shift could decrease growth rates (Sweka and Hartman 2001a) and brook trout may avoid these microhabitats because they have a higher chance of catching the prey species, using less energetically taxing strategies, outside this range. Aquatic community composition reflects these changes in the distribution of prey and predatory species associated with turbidity (Blaber and Blaber 1980; Rodriguez and Lewis 1997), with a greater presence of smaller prey species in turbid water rather than large, visual piscivores.

This experiment focused solely on the sensory modality of vision and showed that stickleback possesses a sensory advantage within 0-5 NTU. However, in the natural environment, predator and prey species can utilize many other sensory cues such as sound, smell, and touch (Abrahams 2005). The availability of multiple sensory cues in the natural environment may give stickleback a different sensory advantage than I observed in this experiment. Turbidity reportedly does not affect foraging rates of stickleback (Webster et al. 2007) as a result of their ability to depend on olfactory cues. However, increased turbidity can impact the visually-based component of mate choice in sticklebacks. Engström-Öst and Candolin (2006) reported that increased turbidity caused female stickleback to pay attention to males in turbid water only if they courted significantly more than males in clear water. Although that study highlighted the

significant role of courtship displays and red colouration in mate selection (Rowland 1989; Milinski and Bakker 1990), the final spawning decision of the females in the experiment did not depend on turbidity, but instead on a nonvisual cue unrelated to turbidity (Engström-Öst and Candolin 2006). Their ability to detect prey and not influence mate choice, as well as the visual sensory advantage to detect predators between 0-5 NTU, may lead to sticklebacks maintaining or increasing the range of turbidity values in which they gain a sensory advantage over a visual predator. Determining the specific range of turbidity that provides a sensory advantage to stickleback over a predator in natural, turbid conditions, while not impacting their prey and mate detection abilities, requires further research using different combinations of sensory stimuli. Such research would provide further insight into the sensory modalities that lead to prey preference for turbid water.

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Tables:

Table 2.1 Swimming behaviours of brook trout and three-spined stickleback. These behaviours are descriptive representations of the baseline behaviour of the species displayed in the absence of a stimulus and how each species reacted when they detected a stimulus.

Species	Baseline Behaviour	Reactive Behaviour
Three-spined stickleback	Slow, smooth swimming with pauses	Direct, rapid advance towards the stimulus for more than 1-2cm (Giles and Huntingford 1984)
	Remain stationary at surface, bottom or in water column	Direct, rapid movement away from the stimulus for more than 1-2cm (Giles and Huntingford 1984)
	Slow, vertical ascent to water surface	
Brook trout	Resting, immobile on gravel bottom	Orientation of head and then body towards the stimulus (Sweka and Hartman 2001b),
	Freely swimming in tank with no rapid orientations	Rapid movement towards the stimulus (personal observation)

Table 2.2 Results from the pairwise post hoc (Tukey method) comparisons to determine the intraspecific effects of different levels of turbidity on detection of a visual stimulus.

Species	Comparison	Difference	t ratio	df	p	lower CL	upper CL
Stickleback	0-5	0.05	1.37	70	0.65	0.01	0.08
	0-10	**0.11**	**3.17**	**70**	**0.02**	**0.07**	**0.14**
	0-15	**0.19**	**5.66**	**70**	**<0.01**	**0.16**	**0.23**
	0-20	**0.24**	**7.02**	**70**	**<0.01**	**0.21**	**0.27**
	5-10	0.06	1.80	70	0.38	0.03	0.10
	5-15	**0.15**	**4.29**	**70**	**<0.01**	**0.11**	**0.18**
	5-20	**0.19**	**5.66**	**70**	**<0.01**	**0.16**	**0.23**
	10-15	0.09	2.49	70	0.11	0.05	0.12
	10-20	**0.13**	**3.85**	**70**	**<0.01**	**0.10**	**0.17**
	15-20	0.05	1.37	70	0.65	0.01	0.08
Trout	**0-5**	**0.10**	**8.03**	**68**	**<0.01**	**0.09**	**0.12**
	0-10	**0.15**	**11.50**	**68**	**<0.01**	**0.13**	**0.16**
	0-15	**0.17**	**13.45**	**68**	**<0.01**	**0.16**	**0.19**
	0-20	**0.19**	**14.97**	**68**	**<0.01**	**0.18**	**0.20**
	5-10	**0.04**	**3.47**	**68**	**0.01**	**0.03**	**0.06**
	5-15	**0.07**	**5.42**	**68**	**<0.01**	**0.06**	**0.08**
	5-20	**0.89**	**9.94**	**68**	**<0.01**	**0.88**	**0.90**
	10-15	0.03	1.95	68	0.30	0.01	0.04
	10-20	**0.04**	**3.47**	**68**	**0.01**	**0.03**	**0.06**
	15-20	0.02	1.52	68	0.55	0.01	0.03

Figures:

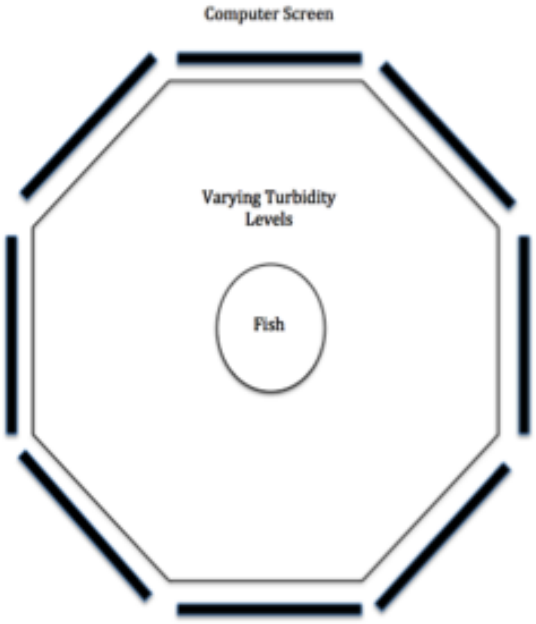

Figure 2.1 Schematic of the experimental tank used for turbidity trials. Fish were kept in the circular interior tank while I manipulated turbidity in the outer octagonal tank. Eight computer screens surround the tank, each displaying an empty aquarium.

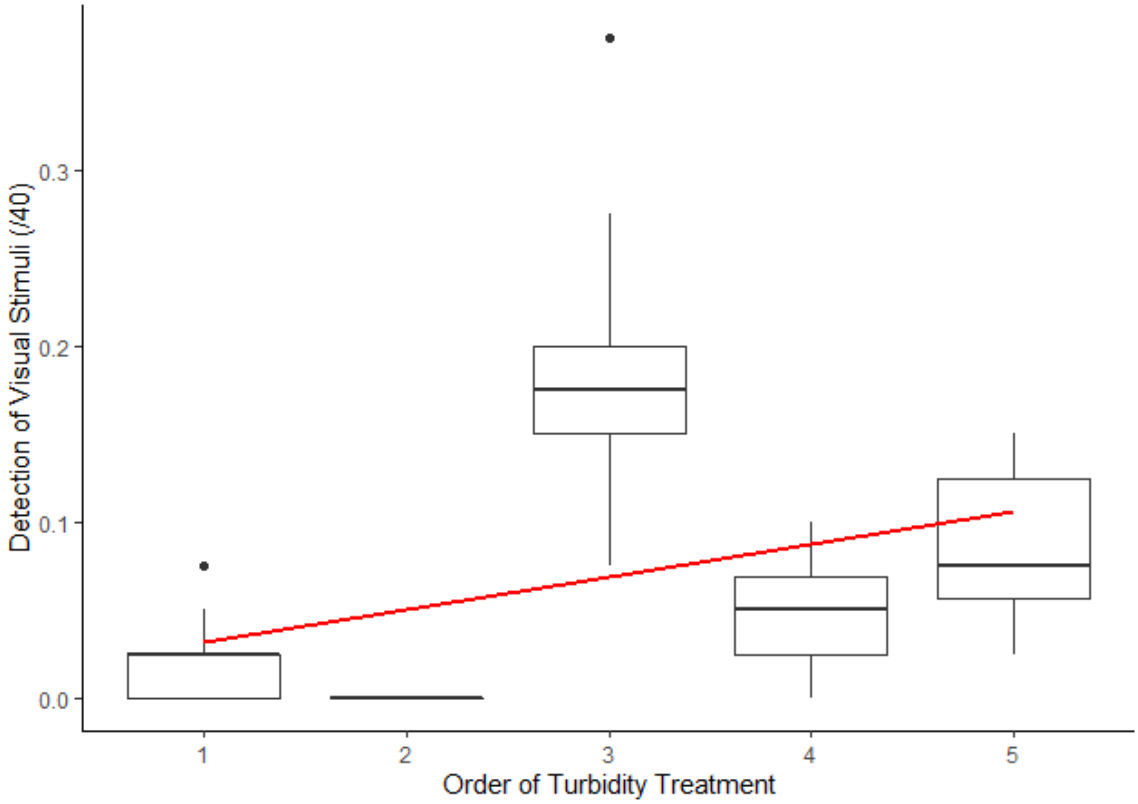

Figure 2.2 Detection of a visual stimulus (out of n=40) for brook trout as a response to the order of turbidity treatments (15 NTU, 20 NTU, 0 NTU, 10 NTU, 5 NTU). The boxplot shows the median (line), the interquartile range (IQR 25 and 75%), whiskers represent the next quartile of the data (1.5*IQR), and black closed circles represent outliers. The red line indicates the line of best fit.

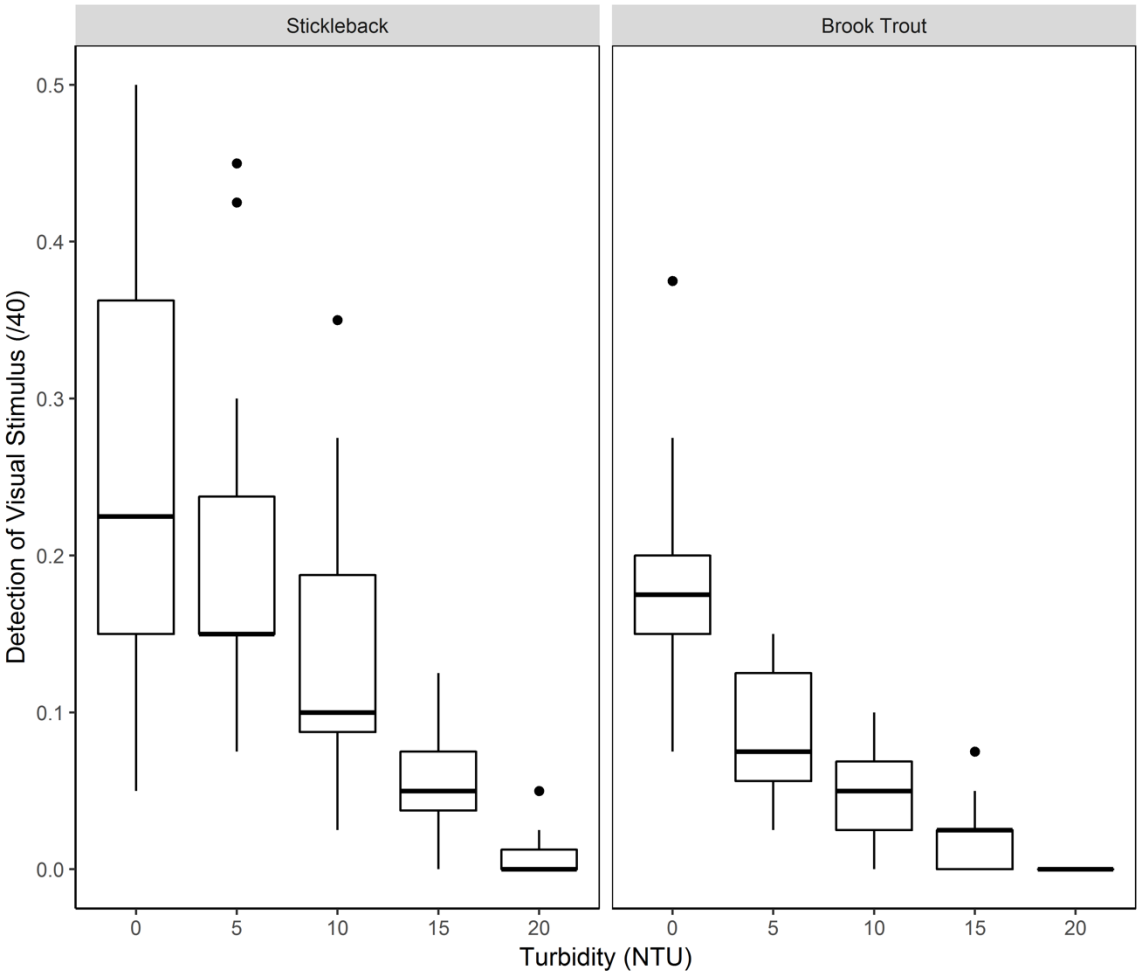

Figure 2.3 Detection (positive response to the presentation of the stimulus) of a visual stimulus (out of n=40) for three-spined stickleback and brook trout at 5 different turbidity levels (NTU). The boxplot shows the median (line), the interquartile range (IQR 25 and 75%), whiskers represent 1.5*IQR, and black closed circles represent outliers.

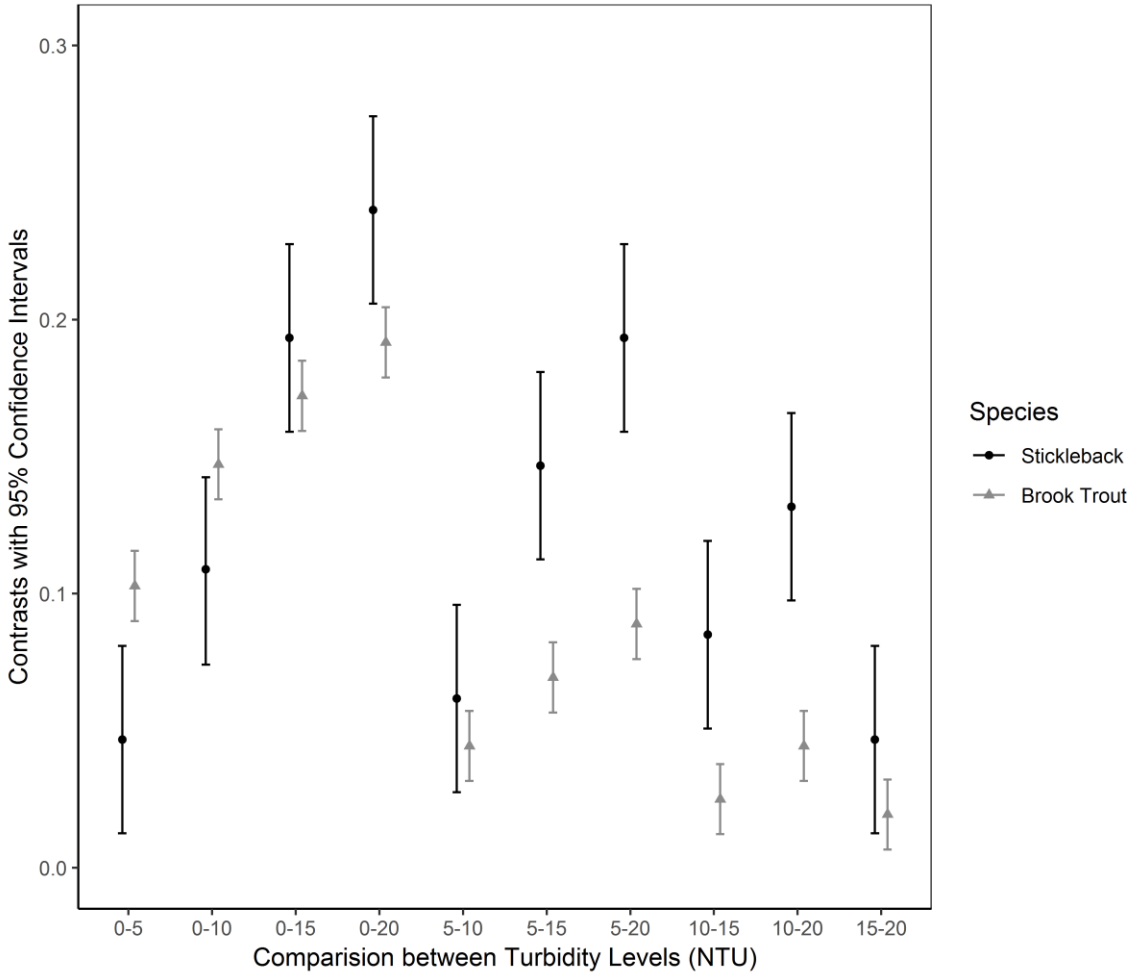

Figure 2.4 Interspecific comparison of responses in detection of visual stimuli to changes in turbidity. Pairwise contrasts with 95% confidence intervals (CIs) were calculated based on the separate analysis of the post-hoc testing of the difference in the mean detections between two treatments for each species model. CIs that do not overlap are assumed to have a p-value of <0.05 and differ significantly.

Chapter 3 : Reservoirs, sensory systems, and fish biodiversity: A meta-analysis on the impact of turbidity on visual and non-visual fish species

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Abstract

The diversity of a species' sensory systems partially results from the vast ranges of sensory environments created by physical, chemical, and biological properties within aquatic ecosystems. However, any modifications to the sensory environment, such as a change in turbidity that impacts visual acuity, could influence which sensory systems provide organisms with the most significant competitive benefit. Furthermore, these changes can accumulate and lead to systematic changes in community composition. Whereas many past studies examined how changes to the environment influence community composition, how the primary sensory mechanisms of species within a community can influence shifts in composition remains unknown. I conducted a meta-analysis of published studies to investigate shifts in community composition associated with modifications to turbidity from the creation of reservoirs. Examination of pre-and post-impoundment biodiversity of the overall community, as well as proportions of visual and non-visual species, provided a broader understanding of the potential impacts that visual information change may have on aquatic community composition. Specifically, I detected a significant relationship between turbidity and both Shannon-Weiner biodiversity and evenness of the visual subset of the community, with decreases in these biological indicators as turbidity increased. Turbidity and the biodiversity of the non-visual subset also interacted significantly, with biodiversity increasing as turbidity increased. This understanding can facilitate future prediction of the type and magnitude of changes expected when turbidity alters the visual sensory environment.

KEYWORDS: Meta-analysis, dams, reservoirs, turbidity, biodiversity, visual, sensory systems, habitat change

Introduction:

Fish species have adapted to the vast ranges of fluctuating physical, chemical, and biological properties within aquatic habitats across the globe. Each of these habitats contains unique ranges of properties such as dissolved oxygen concentrations, temperature gradients, nutrient cycling, salinity, and turbidity levels (Carpenter et al. 2011), and these environmental properties can influence the perception of signals and the resulting behaviours of aquatic species (Endler 1992; Cummings and Endler 2018; Fuller and Endler 2018). These species adaptations can be behavioural (e.g., diel migration for feeding, Loose and Dawidowicz 1994), physiological (e.g., facultative air-breathing in the armoured catfish (*Hoplosternum littorale,* Brauner et al. 1995), or involve adaptations to the species' sensory systems (e.g., high density of taste buds on the barbels for non-visual feeding, Harvey and Batty 1998). If an environment is altered to become less visual, then a specialized non-visual sensory system can give a species a competitive advantage over a species that evolved in a visual environment with a different suite of sensory capabilities (Janssen 1997, Bergstrom and Mensinger 2009, Nurminen et al. 2010, Abrahams et al. 2017). Due to the multitude of different aquatic habitats on Earth, many fish species have evolved diverse sensory systems.

Differences in sensory systems can reflect fishes adaptations to its habitat's sensory environment, as the systems become "tuned" to match that environment's characteristics (Endler 1992; Cummings and Endler 2018; Fuller and Endler 2018). Fishes in aquatic environments use electrical, auditory (including pressure), chemical,

and visual sensory systems (Abrahams 2005). Species survival may hinge upon their sensory systems efficacy because sensory systems largely define an individual's ability to find prey, avoid predation, and select mates and microhabitats. In particular, many fishes use vision as their primary sense (Domenici 2002; Jönsson et al. 2013), emphasizing the importance of vision-related sensory cues in aquatic habitats. A specialized suite of sensory systems, well adapted to their environment, dramatically enhances a species chances of outcompeting species that lack the same specialized sensory abilities for those conditions. However, issues arise when the physical characteristics of the environment change, redefining which sensory systems best suit that environment.

Although changes to the physical characteristics of the environment can occur naturally, anthropogenic impacts on aquatic ecosystems can also rapidly change physical conditions, thereby impacting the habitat's sensory environment. These anthropogenic impacts can also drive changes in biodiversity (Vitousek 1994; Sala et al. 2000; Revenga et al. 2005; Dudgeon et al. 2006; Ferrari 2014) and include overexploitation, water pollution, flow modification, habitat destruction or degradation, and invasion of exotic species (due to accidental or intentional introduction) (Allan and Flecker 1993; Naiman and Turner 2000; Sala et al. 2000; Jackson et al. 2001; Malmqvist and Rundle 2002; Dudgeon et al. 2006; Revenga et al. 2005).

The creation of dams and their associated reservoirs represents a common anthropogenic occurrence that combines multiple adverse impacts on aquatic ecosystems. Their impacts include increases in temperature, changes in levels of methylmercury,

sedimentation, decreased dissolved oxygen, and changes in water turbidity (Rosenberg et al. 1997), with the latter changing the light environment (i.e., the sensory environment). This type of change to the sensory environment can cause a shift in the composition of the fish community as a result of modifications to the efficacy of sensory systems (Rodriguez and Lewis 1997; Tejerina-Garro et al. 1998).

Increased turbidity alters the sensory environment, which can impact vision; however, when vision is hindered or performing poorly, other senses may compensate (Hartman and Abrahams 2000; Abrahams 2005). These other senses may result in a fish species reliance on non-visual sensory cues to outcompete visually-dependent species when visibility is reduced in the environment. In this case, different species, utilizing a different suite of sensory systems, may have a sensory advantage (Bergstrom and Mensinger 2009) given adaptions specific to the changed habitat conditions. The impact of these more efficient species may displace native species from their native habitats (Race 1982; Douglas et al. 1994). Displacement of key species may then change the overall biodiversity of the habitat.

The objective of this chapter is to determine whether a change in turbidity levels results in a systematic change in the composition of resident fish species communities. To measure the composition of the resident fish species communities, I chose the Shannon-Wiener Index, which takes into account species richness, defined as the number of species in an area, and evenness that is defined as how equitably individuals are distributed among species within a community (Wilsey and Potvin 2000; Stirling and

Wilsey 2001). However, these two components can be independent of each other (Stirling and Wilsey 2001) or work in opposite directions with potentially confounding effects (Bianchi et al. 2000; Kimbro and Grosholz 2006). These confounding effects can result in diversity significantly changing without changes to evenness, or richness, and vice versa. As such, I considered both the evenness and species richness of the pre- and post-impoundment communities. I predicted that increased turbidity leads to decreased biodiversity of visual species as a result of decreased sensory information in visual species. I also predicted that overall species biodiversity would decrease in response to either increased or decreased turbidity. I based this prediction on the alteration of the natural sensory environment shifting natural species dynamics, which can impact community biodiversity. To answer this question, I undertook a global meta-analysis to examine the composition of fish communities before and after the creation of a reservoir.

Methods:

Literature Review:

Using the search engines Web of Science, SCOPUS, and Google Scholar, I found 2,303 peer-reviewed studies using the search terms "biodiversity OR richness" AND "dam* OR impoundment OR reservoir*". I also reviewed all relevant references cited in these publications to determine whether they met key selection criteria – namely that they: (1) provided abundance data for the entire fish community pre- and post impoundment; and (2) the provided abundances were broken down for each species of fish within the community; I omitted reports that focussed solely on abundance changes

of a single species. The selection criteria allowed species abundance data reported as either raw data or as graphs, where I could extract the data using DATA THIEF v1.7 (Tummers 2006). To determine whether the studies met the selection criteria, I first analyzed the abstracts to evaluate whether they referred to changes to the biotic community or changes due to impounding. If the paper referred to either of these changes, I then read the paper to determine whether the studies met the criteria. Two exceptions were made regarding the papers I chose to include: "Response by fish assemblages to an environmental flow release in a temperate coastal Australian river: a paired catchment analysis." (Rolls et al. 2011) which performed a paired analysis between similar-sized regulated and unregulated tributaries within the Paterson and Williams sub-catchments, because they used the paired unregulated reservoir as an example of the pre-impoundment conditions; and "Resident fish assemblages in a Columbia River impoundment" (Barfoot et al. 2002), which compared data between 1984-85 to 1995. The 1984-85 data were collected after the dam was impounded; however, the study reported these abundances to be similar to the composition pre-impoundment, and as such, I included it in the analysis. I initially required studies that included turbidity data, as well as other abiotic variables such as temperature and dissolved oxygen, and pre- and post-impoundment. However, a lack of reporting on turbidity in the studies that met the other two requirements necessitated that I relax this criterion and obtain turbidity information through other sources. This strategy yielded an initial total of 20 studies that reported on fish communities within 26 dam locations.

A lack of studies that included information for turbidity pre- or post-impoundment necessitated further research on the dams and reservoirs to determine the degree of change in turbidity within the reservoirs. For each of the 26 dam sites that were highlighted in the initial study search, I searched for pre- and post-impoundment turbidity data using primary literature searches, online databases, and government websites such as the United States geological survey (USGS) (Appendix A). For the dams lacking pre-impoundment turbidity information, due to the age of the dam or lack of recording of turbidity, I used the turbidity values upstream of the reservoir during a time frame that was representative of when the fish community information was collected; the upstream turbidity values should offer the closest approximation of pre-impoundment conditions. In instances where I could not find pre- and post-impoundment turbidity, I removed the dam site from the meta-analysis, reducing the number of dams included in this analysis to 13. Other physical characteristics were initially included in the analysis (i.e. temperature and dissolved oxygen); however, given the limited availability of this data for both periods, I did not wish to limit the sample size further by removing dams lacking that data. Therefore turbidity data was the only physical characteristic included in the meta-analysis, which included a total of 11 studies that reported on fish communities in 13 dam sites (Appendix B). Details on the study's sampling techniques, sampling effort, and time of sampling for these 13 locations were also recorded (Appendix C).

Determining Visual vs. Non-Visual Fish Species:

I determined the primary sensory system using the information on fish species available at FishBase (http://www.fishbase.org). The websites Global Invasive Species

Database (http://www.issg.org/database) and the Center for Community Mapping (http://www.comap.ca) also provided sources of supplementary information, as did the primary literature research on the species. From the information available, I concluded whether each species depended primarily on visual or non-visual sensory clues in its native habitat, thus designating them as visual or non-visual species, respectively.

I categorized each fish as visual or non-visual by examining characteristic features of the species (e.g., the diameter of the eye in relation to the size of the head, feeding time of day, specialized sensory organs for olfaction and electrolocation). I chose these characteristics as they were commonly available in the literature and could be extracted for most fish species (or a closely-related species). I then applied a flow chart to each species (Figure 3.1) in order to classify whether a species used a visual or non-visual primary sense. Non-visual species include those with an eye diameter of less than 10% of head length (Pankhurst 1989; Fishelson et al. 2004). Species with eye diameters between 10- 25% of their head length were classified as non-visual if they were nocturnal demersal feeders (Bassett and Montgomery 2011), and/or olfactory specialists, that is a species that has thousands of taste buds located on the exterior of the fish body, fins, barbells and lip papillae (Bardach et al. 1967; Kasumyan and Doving 2003), and/or weakly electric fish using a specialized electric organ (von der Emde 2006; von der Emde and Fetz 2007). Species with an eye diameter greater than 25% of their head length were classified as visual (Pankhurst 1989; Fishelson et al. 2004). Species with an eye diameter between 10-25% of their head length were classified as visual if they were not nocturnal demersal feeders or olfactory specialists, or lacked specialized electric organs for active

electrolocation. In study species with insufficient information available to complete the flow chart, I instead used a closely related species as a proxy. This methodology was only required for two species (less than 1%), both of which were within the Cyprinidae family (striped shiner, *Luxilus chrysocephalus,* substituted for the duskystripe shiner, *Luxilus pilsbryi*; the bigeye shiner, *Notropis boops,* substituted for the Arkansas River shiner, *Notropis girardi*).

Data Analysis:

In order to determine species biodiversity for pre- and post-impoundments for each dam, I calculated the Shannon-Wiener Diversity Index, a measure of community composition that includes species richness and evenness (Shannon and Weaver 1949; Pielou 1966a; Whittaker 1972; Spellerberg and Fedor 2003). I chose this diversity index because it is the most commonly used metric in ecological papers (Buddle et al. 2005), is commonly used to quantify biological diversity within communities (Sherwin et al. 2006), and adequately measures diversity to assess trends and changes in time (Buckland et al. 2005). Calculation of this index uses the equation:

$$H' = -\sum_{i=1}^{S} p_i * \ln(p_i)$$

where: *H'* is the Shannon diversity index, p_i, is the relative frequency of species *i* in the community, and *S* is the species richness calculated as the number of species in that community.

I determined species richness, *S*, while calculating the Shannon-Weiner diversity index. However, because the Shannon-Wiener diversity index condenses species richness and evenness, I also calculated Pielou's index of species evenness (*J)* (Pielou 1966b; Jost 2010) using the equation:

$$J = H'/\ln(S)$$

I calculated these three variables (S,H', and J) for the pre- and post-impoundment for the entire fish community, as well as for both visual and non-visual fish species separately.

To determine the impact of changing turbidity through impoundment on species composition, I calculated the change in turbidity as well as the change in biodiversity, evenness, and species richness by subtracting the post-impoundment values from the pre-impoundment values. I then tested the change in each variable using linear regression to determine whether the change in turbidity associated with the impoundment of the reservoir impacted the biological variables. As each dam was measured pre and post-impoundment, Dam ID was also included as a random effect to account for this variability. Initially, an analysis of variance (ANOVA) was used to determine whether turbidity explained the differences in the variables; however, it revealed many outliers, and the sample size was small (n=13). Therefore, I modified my approach by analyzing the pre- and post-impoundment data points separately rather than focusing on the calculated difference in the data. This approach allowed me to investigate potential interactions between turbidity and each of the biological variables (biodiversity, evenness, and species richness) separately and investigate the impact of damming on the

variables. To this end, I used a linear mixed-effects model (LMM) with Dam ID included as a random variable, for the analysis of biodiversity, evenness and species richness data. To evaluate differences in biodiversity, evenness, and species richness, I performed an analysis of deviance on the LMM. The analysis of the data was conducted in R version 3.3.3 (R Core Team 2013) using the car (Fox and Weisberg 2019) and lme4 (Bates et al. 2015) packages. Results were considered statistically significant for p-values less than 0.05.

Results:

This meta-analysis included a total of 248 species, classifying 193 as visual (Table 3.1) and 55 as non-visual (Table 3.2). Eleven out of the 55 species classified as non-visual had eye diameters less than 10 % of their head length, 37 were nocturnal, demersal feeders, four were olfactory specialists, and three used their specialized electric organ for active electrolocation. Eighty-two of the 193 visual species had eye diameters greater than 25 % of their head length, and 111 species were neither a nocturnal demersal feeder, olfactory specialist, or species with specialized electric organs for active electrolocation.

The impact of dams on turbidity varied. In four of the 13 dams studied, river impoundment increased reservoir turbidity, while turbidity decreased in the other nine dams (Table 3.3). Given a lack of information on other abiotic variables, I omitted data on changes in other physical characteristics in the analysis and focussed only on changes in turbidity. However, these changes in turbidity did not follow any geographical or climatic trends.

An analysis of variance on the linear model revealed no significant effect of changes in turbidity on changes in biodiversity of the entire community ($F_{(1, 11)} = 1.22$, p=0.29), the visual subset ($F_{(1, 11)} = 1.37$, p=0.27), or the non-visual subset ($F_{(1, 11)} =$ >0.01, p=0.97). Turbidity change also had no significant effect on the changes in evenness of the entire community ($F_{(1, 11)} = 1.70$, p=0.22), the visual subset ($F_{(1, 11)} =$ 1.21, p=0.30), or the non-visual subset ($F_{(1, 11)} = 0.13$, p=0.73). Finally, turbidity change had no significant effect on changes in species richness of the entire community ($F_{(1, 11)} =$ 0.14, p=0.72), the visual subset ($F_{(1, 11)} = 0.06$, p=0.81), or the non-visual subset ($F_{(1, 11)} =$ 0.39, p=0.54).

For the pre- and post-impoundment data points, an analysis of deviance on the linear mixed-effect model showed a significant relationship between turbidity and biodiversity ($\chi^2_{(1, 25)} = 6.26$, p=0.01) (Table 3.4) as well as turbidity and evenness ($\chi^2_{(1, 25)} = 6.77$, p=0.01) within the visual subset of the community (Table 3.5). As turbidity increased, biodiversity and evenness in the visual subset both decreased. There were no significant interactions between turbidity and species richness within the entire community, visual subset, and non-visual subset (Table 3.6). There were also no significant interactions between turbidity pre- and post-impoundment except for biodiversity within the non-visual subset of the community ($\chi^2_{(1, 25)} = 6.31$ p=0.01).

Discussion:

My study demonstrated significant changes in biodiversity and evenness within the subset of species that rely upon vision as their primary sense. The reservoir communities with higher turbidity were associated with lower biodiversity and evenness

within the visual subset, than with clearer water, lower turbidity communities. In clearer water, fishes use their visual sensory adaptations in order to compete for food, shelter, and mate selection. When increased turbidity decreases the quality of visual cues, visual species may be unable to utilize the decreased sensory information, thus causing them to function at a lower level than in clearer water. Those species may then either leave the area or remain, potentially facing elevated competition from better-adapted species. This competition may then lead to decreased growth and mating rates in visual species, thereby decreasing the contribution of this species subset to biodiversity and evenness.

When turbidity increases, the amount of visual information available for a species to use decreases (Utne-Palm 2002). This phenomenon can impact species diversity within aquatic ecosystems by influencing reproduction, predator-prey dynamics, and competition. Colour vision illustrates one such way that turbidity limits reproduction by affecting the colour-dependent sexual selection of mates, as reported in cichlid fish species of Lake Victoria (Seehausen et al. 1997). Additionally, a change in turbidity can influence the sensory modality of which cues fishes rely upon most heavily during mate choice selection. An example of this phenomenon was reported for three-spined stickleback (*Gasterosteus aculeatus*), where females shifted their reliance towards olfactory rather than visual cues in turbid water (Heuschele et al. 2009). These changes in sexual selection preferences have potential consequences for the viability of populations, thereby decreasing species diversity.

Altering turbidity can impact predator-prey dynamics. Increased turbidity decreases species reaction distances for both predator and prey recognition, as seen with pike (*Esox Lucius*) and roach (*Rutilus rutilus*) (Ranåker et al. 2012). This change in reaction distance can also alter the type of prey selected by the predator, as seen with largemouth bass (*Micropterus salmoides),* whose prey selection became less specialized as turbidity increased (Shoup and Wahl 2009); these changes then impacted the vulnerability of prey at different turbidity levels and caused changes to the trophic interactions within the ecosystem (Shoup and Wahl 2009). Alteration of predator-prey dynamics also affects the ability of both parties to compete, thereby impacting community biodiversity.

Decreases in a visual species' ability to compete may create an opportunity for a species adapted to the new turbidity level to invade (Janssen 1997; Bergstrom and Mensinger 2009; Nurminen et al. 2010; Abrahams et al. 2017), potentially leading to further decreases in ecosystem biodiversity. These invasions can reflect newly-introduced species, or a native species historically present in low numbers, such as the blacknose dace (*Rhinichthys atratulus)* and creek chub (*Semotilus atromaculatus*) in the highland regions of the Southeastern United States (Scott and Helfman 2001). These better-adapted species may have a competitive edge over the visually-dependent native species compromised by the increased turbidity, potentially leading to further population declines, while biodiversity of non-visual species increases. This phenomenon was reported in populations of the non-visually adapted ruffe (*Gymocephalus cernua)* and visually adapted perch (*Perca fluviatilis)*, where abundances of perch declined and ruffe

increased with an increase in turbidity (Bergman 1991). Determining whether the now dominant species at specific sites were invasive or previously native but subordinate in the habitat requires further research. Furthermore, changes in biodiversity may result from a key prey species no longer able to survive in the changed environment or could result from a non-fish species exploiting the newly created niche. Further examination of these phenomena requires additional studies on ecosystems currently experiencing a change in turbidity linked to a dam's implementation.

At low turbidity, the negative impacts of turbidity on reproduction, predator-prey dynamics, and competition decreases for visual species (Vinyard and O'Brien 1976; Utne-Palm 2002; Shoup and Wahl 2009). Higher evenness and biodiversity rates could occur through changes in predatory foraging rates and prey selectivity. This decrease in prey selectivity may reflect the reduced difficulty in capturing rapidly moving prey species. Increased turbidity constrains the type of prey that predators can capture, thereby decreasing the abundance of those species while increasing an abundance of species that evade capture (Shoup and Wahl 2009; Carter et al. 2010; Figueiredo et al. 2016), resulting in an unevenly distributed community. However, lower turbidity levels mitigate this pressure on predation, and predators decrease their prey selectivity, thereby allowing the abundances of prey species to equalize, and the community to become more even (Figueiredo et al. 2016). This shift toward an even community can occur with decreasing or increasing abundances. Further work could examine how species abundances may shift in either direction when turbidity decreases in those habitats. Also, an increase in

evenness may reflect an influx of new species or an increase in formerly rare species. To ascertain what influences these changes requires further studies on species interactions.

In summary, my meta-analysis links higher turbidity levels with lower biodiversity and evenness within visually adapted species. These relationships between turbidity and biodiversity metrics were not associated with the changes to the reservoirs associated with an impoundment; as such, the results are not consistent with our hypothesis that a change in the physical environment can lead to a systematic change in fish community composition. This non-significant result may reflect the low statistical power of my tests associated with the small sample size (n=13). A change to the physical environment that causes a species to no longer be successful because they are outcompeted by species that have better adaptations has been seen with invasions, where the invasive species is better adapted to the environment. For example, the non-visually-adapted invasive western mosquitofish (*Gambusia affinis*) outcompetes the native, visually-adapted inanga (*Galaxis maculatus*) (Abrahams et al. 2017). By understanding how a change in the physical environments can affect a fish community, we may be able to further predict how the entire fish community composition may change in response to anthropogenic effects such as the creation of a dam and its corresponding impoundment.

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Tables:

Table 3.1 List of species classified as visual

Family	Scientific Name	Family	Scientific Name
Acestrorhynchidae	*Acestrorhynchus falcatus*	**Cyprinidae**	*Luxilus pilsbryi*
	Acestrorhynchus microlepis		*Luxilus chrysocephalus*
Anostomidae	*Anostomus brevior*		*Luxilus cornutus*
	Leporinus fasciatus		*Macrhyboposis aestivalis*
	Leporinus friderici		*Macrhybopsis marconis*
	Leporinus gossei		*Nocomis biguttatus*
	Leporinus granti		*Notemigonus crysoleucas*
	Leporinus maculatus		*Notropis amabilis*
Atherinopsidae	*Labidesthes sicculus*		*Notropis amblops*
	Menidia beryllina		*Notropis atherinoides*
	Odontesthes bonariensis		*Notropis boops*

Auchenipteridae	*Auchenipterus nuchalis*		*Notropis buchanani*
Balitoridae	*Lepturichthys fimbriate*		*Notropis girardi*
Catostomidae	*Carpiodes carpio*		*Notropis greenei*
	Carpiodes cyprinus		*Notropis nubilus*
	Carpiodes velifer		*Notropis ozarcanus*
	Catostomus		*Notropis rubellus*
	Catostomus commersonii		*Notropis stramineus*
	Catostomus discobolus		*Notropis volucellus*
	Catostomus latipinnis		*Phenacobius mirabilis*
	Catostomus platyrhynchus		*Pimephales notatus*
	Hypentelium nigricans		*Pimephales promelas*
	Moxostoma carinatum		*Pimephales tenellus*

	Moxostoma congestum		*Pimephales vigilax*
	Moxostoma duquesnei		*Platygobio gracilis*
	Moxostoma erythrurum		*Rhinichthys cataractae*
	Moxostoma macrolepidotum		*Rhinichthys osculus*
Centrarchidae	*Ambloplites constellatus*		*Rhinogobio cylindricus*
	Ambloplites rupestris		*Rhinogobio typus*
	Lepomis auratus		*Rhinogobio ventralis*
	Lepomis cyanellus		*Rhodeus sericeus*
	Lepomis gibbosus		*Rutilus*
	Lepomis gulosus		*Saurogobio dabryi*
	Lepomis macrochirus		*Semotilus atromaculatus*
	Lepomis megalotis		*Squalius pyrenaicus*
	Lepomis microlophus	**Cyprinodontidae**	*Cyprinodon rubrofluviatilis*

	Micropterus dolomieu	**Eleotridae**	*Gobiomorphus australis*
	Micropterus punctulatus		*Gobiomorphus coxii*
	Micropterus salmoides		*Philypnodon grandiceps*
	Micropterus treculii	**Erythrinidae**	*Hoplerythrinus unitaeniatus*
Characidae	*Astyanax altiparanae*		*Hoplias aimara*
	Astyanax bifasciatus	**Esocidae**	*Esox lucius*
	Astyanax bimaculatus	**Fundulidae**	*Fundulus catenatus*
	Astyanax dissimilis		*Fundulus kansae*
	Astyanax gymnodontus		*Fundulus olivaceus*
	Astyanax minor		*Fundulus sciadicus*
	Bryconamericus ikaa		*Fundulus zebrinus*
	Charax pauciradiatus	**Hemiodontidae**	*Bivibranchia bimaculata*
	Cyphocharax helleri		*Hemiodus quadrimaculatus*

	Jupiaba keithi		*Hemiodus unimaculatus*
	Jupiaba meuniere	**Hiodontidae**	*Hiodon alosoides*
	Moenkhausia chrysargyrea		*Hiodon tergisus*
	Moenkhausia georgiae	**Iguanodectidae**	*Bryconops affinis*
	Moenkhausia hemigrammoides		*Bryconops caudomaculatus*
	Moenkhausia oligolepis		*Bryconops melanurus*
	Moenkhausia surinamensis	**Loricariidae**	*Curimata cyprinoides*
	Oligosarcus longirostris	**Moronidae**	*Morone chrysops*
	Poptella brevispina	**Mugilidae**	*Trachystoma petardi*
Chilodontidae	*Chilodus zunevei*	**Parodontidae**	*Apareiodon vittatus*
Cichlidae	*Cichlasoma bimaculatum*	**Percichthyidae**	*Macquaria novemaculeata*

	Crenicichla iguassuensis		*Siniperca knerii*
	Crenicichla saxatilis	**Percidae**	*Etheostoma blennioides*
	Cteniloricaria maculate		*Etheostoma caeruleum*
	Geophagus brasiliensis		*Etheostoma euzonum*
	Geophagus surinamensis		*Etheostoma juliae*
	Krobia guianensis		*Etheostoma punctulatum*
	Satanoperca jurupari		*Etheostoma spectabile*
Clupeidae	*Dorosoma cepedianum*		*Etheostoma stigmaeum*
	Dorosoma petenense		*Etheostoma zonale*
Cottidae	*Cottus bairdii*		*Perca flavescens*
	Cottus carolinae		*Perca fluviatilis*
	Cottus gobio		*Percina apristis*
	Cottus hypselurus		*Percina caprodes*

Curimatidae	*Cyanocharax aff alburnus*		*Percina carbonaria*
	Cyphocharax santacatarinae		*Percina evides*
	Cyphocharax spilurus		*Percina nasuta*
	Cyprinella galactura		*Stizostedion vitreum*
Cyprinidae	*Abbottina obtusirostris*	**Percopsidae**	*Percopsis transmontana*
	Abramis brama	**Petromyzontidae**	*Eudontomyzon mariae*
	Acrocheilus alutaceus		*Ichthyomyzon gagei*
	Alburnus alburnus	**Poeciliidae**	*Gambusia affinis*
	Blicca bjoerkna		*Gambusia holbrooki*
	Campostoma anomalum		*Poecilia latipinna*
	Carassius auratus	**Pseudomugilidae**	*Pseudomugil signifer*
	Chondrostoma nasus	**Retropinnidae**	*Retropinna semoni*

	Chrosomus erythrogaster	**Salmonidae**	*Oncorhynchus clarki*
	Cyprinella lutrensis		*Oncorhynchus mykiss*
	Cyprinella venusta		*Prosopium williamsoni*
	Cyprinella whipplei		*Salmo trutta*
	Cyprinus carpio		*Salvelinus fontinalis*
	Erimystax dissimilis	**Sciaenidae**	*Aplodinotus grunniens*
	Gila robusta		*Plagioscion squamosissimus*
	Hybognathus argyritis	**Serrasalmidae**	*Myleus rhomboidalis*
	Hybognathus hankinsoni		*Myleus ternetzi*
	Hybognathus placitus	**Tetrarogidae**	*Notesthes robusta*
	Leuciscus idus	**Triportheidae**	*Triportheus rotundatus*
	Leuciscus leuciscus		

Table 3.2 List of species classified as non-visual

Family	Scientific Name	Family	Scientific Name
Anguillidae	*Anguilla australis*	**Hypopomidae**	*Hypopomus artedi*
	Anguilla reinhardtii	**Ictaluridae**	*Ameiurus melas*
Auchenipteridae	*Parauchenipterus galeatus*		*Ameiurus natalis*
	Tatia intermedia		*Ictalurus punctatus*
	Glanidium ribeiroi		*Noturus albater*
Bagridae	*Leiocassis longirostris*		*Noturus exilis*
	Pelteobagrus nitidus		*Noturus flavater*
	Pelteobagrus vachelli		*Noturus flavus*
Balitoridae	*Jinshaia sinensis*		*Pylodictis olivaris*
Callichthyidae	*Corydors aff. Paleatus*	**Lepisosteidae**	*Lepisosteus osseus*
	Megalechis thoracata	**Loricariidae**	*Hypostomus gymnorhynchus*
Centrarchidae	*Pomoxis annularis*		*Hypostomus myersi*
	Pomoxis nigromaculatus		*Ancistrus hoplogenys*

Cobitidae	*Cobitis taenia*		*Harttia surinamensis*
	Leptobotia elongata		*Lithoxus planquettei*
	Leptobotia taeniops		*Loricaria cataphracta*
Cyprinidae	*Barbus barbus*	**Lotidae**	*Lota lota*
	Coreius guichenoti	**Nemacheilidae**	*Barbatula barbatula*
	Coreius heterodon	**Pimelodidae**	*Pimelodus britskii*
	Gobio gobio		*Pimelodus ornatus*
	Hemibarbus labeo	**Plotosidae**	*Tandanus tandanus*
	Hemibarbus maculatus	**Siluridae**	*Silurus meridionalis*
	Mylocheilus caurinus	**Sternopygidae**	*Eigenmannia virescens*
	Ptychocheilus lucius		*Sternopygus macrurus*
	Ptychocheilus oregonensis		
Doradidae	*Doras carinatus*		

Erythrinidae	*Hoplias malabaricus*	
Heptapteridae	*Pimelodella cristata*	
	Pimelodella geryi	
	Pimelodus ortmanni	
	Rhamdia quelen	

Table 3.3 Pre-and post-impoundment turbidity values for each of the 13 dam sites. For paper ID 2 and 12, multiple dam sites were available and were therefore studied as two separate sites.

Paper ID	Dam Name	Location	Pre-Impoundment Turbidity (NTU)	Post-Impoundment Turbidity (NTU)
1	John Day Dam	Washington, USA	10.5	6.9
2	Sanford Dam	Texas, USA	58.7	14.6
2	Ute Dam	New Mexico, USA	9.2	3.1
3	Petit-Saut Dam	Sinnamary, French Guiana	3.4	3.1
4	Salto Caxias Dam	Parana, Brazil	4	2.7
5	Three Gorge Dam	Hubei, China	100	85
6	Sulejowski Reservoir	Poland	1.9	3.5
7	Taylor Draw Dam	Colorado, USA	12.2	15
8	Canyon Dam	Texas, USA	4.4	6.4
9	Beaver Dam	Arkansas, USA	13.1	3.2
10	Grayrocks Dam	Wyoming, USA	7	6.1

11	Chichester Dam	New South Wales, Australia	3.5	0.1
11	Lostock Dam	New South Wales, Australia	1.4	34.9

Table 3.4 Repeated measures analysis of deviance of Shannon-Wiener biodiversity of the entire community, the visual subset and the non-visual subset as a function of turbidity, where BefAft represents pre- and post-impoundment.

ENTIRE COMMUNITY

	Chisq	**Df**	**Pr(>Chisq)**
TURBIDITY	1.65	1	0.20
BEFAFT	0.00	1	0.95
TURBIDITY:BEFAFT	0.50	1	0.48

VISUAL SUBSET

	Chisq	**Df**	**Pr(>Chisq)**
TURBIDITY	6.26	1	0.01
BEFAFT	0.05	1	0.82
TURBIDITY:BEFAFT	0.12	1	0.73

NON-VISUAL SUBSET

	Chisq	**Df**	**Pr(>Chisq)**
TURBIDITY	2.14	1	0.14
BEFAFT	0.44	1	0.51
TURBIDITY:BEFAFT	6.32	1	0.01

Table 3.5 Repeated measures analysis of deviance of evenness of the entire community, the visual subset and the non-visual subset as a function of turbidity, where BefAft represents pre- and post-impoundment.

ENTIRE COMMUNITY

	Chisq	Df	Pr(>Chisq)
TURBIDITY	1.46	1	0.23
BEFAFT	0.00	1	0.98
TURBIDITY:BEFAFT	0.02	1	0.89

VISUAL SUBSET

	Chisq	Df	Pr(>Chisq)
TURBIDITY	6.77	1	0.01
BEFAFT	0.03	1	0.85
TURBIDITY:BEFAFT	0.39	1	0.53

NON-VISUAL SUBSET

	Chisq	Df	Pr(>Chisq)
TURBIDITY	0.35	1	0.55
BEFAFT	0.02	1	0.89
TURBIDITY:BEFAFT	1.15	1	0.28

Table 3.6 Repeated measures analysis of deviance of species richness of the entire community, the visual subset and the non-visual subset as a function of turbidity, where BefAft represents pre- and post-impoundment.

ENTIRE COMMUNITY

	Chisq	Df	Pr(>Chisq)
TURBIDITY	0.02	1	0.88
BEFAFT	0.86	1	0.35
TURBIDITY:BEFAFT	0.78	1	0.38

VISUAL SUBSET

	Chisq	Df	Pr(>Chisq)
TURBIDITY	0.26	1	0.61
BEFAFT	0.93	1	0.34
TURBIDITY:BEFAFT	0.38	1	0.53

NON-VISUAL SUBSET

	Chisq	Df	Pr(>Chisq)
TURBIDITY	1.26	1	0.26
BEFAFT	0.39	1	0.53
TURBIDITY:BEFAFT	2.33	1	0.13

Figures:

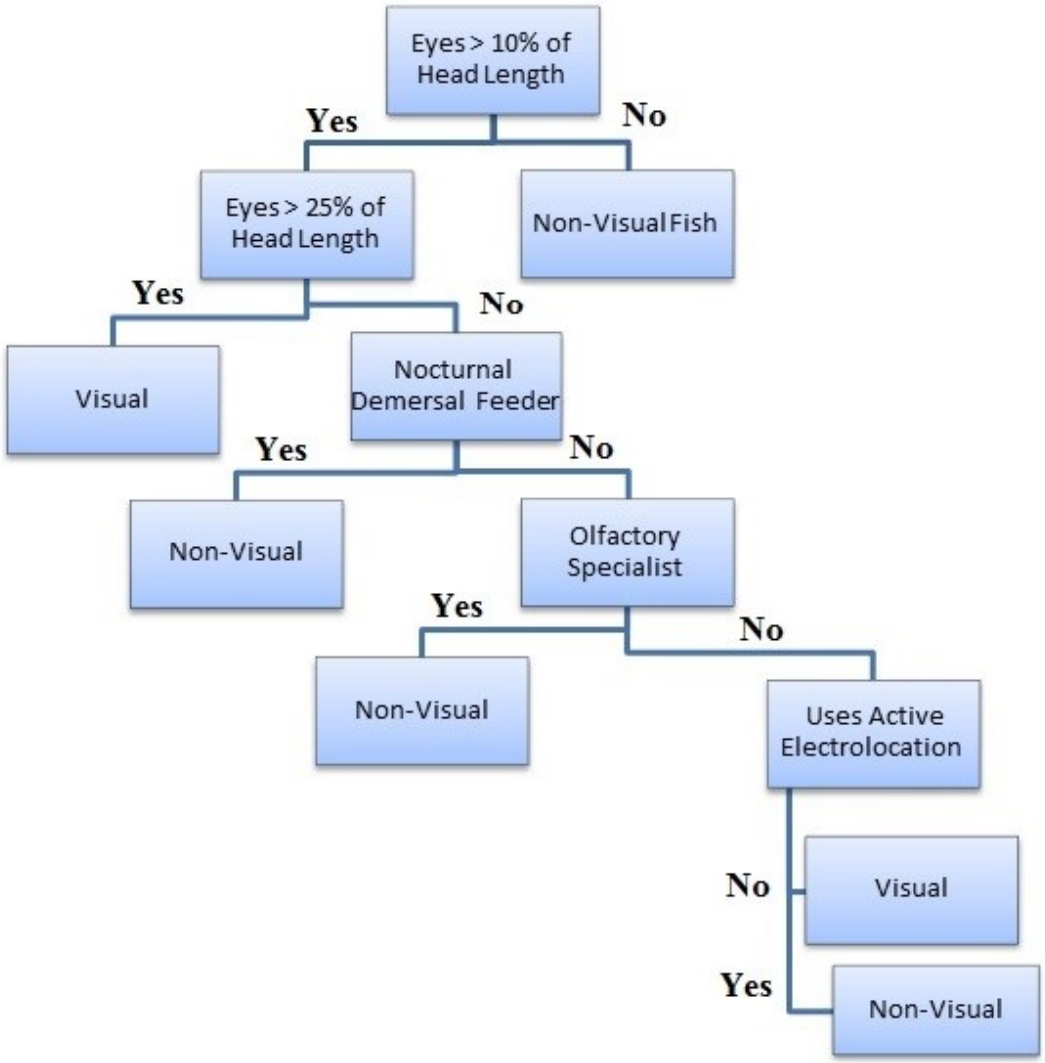

Figure 3.1 Flow chart used to classify fish species as a visual or non-visual species.

Chapter 4 General Conclusions

This thesis's focus was to examine the repercussions of changes in the available sensory information of an aquatic environment on its resident fish species. In particular, I studied the impact of changes in the availability of visual information on both a small (habitat interactions) and a large (community composition structure) scale. The research aimed to gain further insight into the consequences that can occur in aquatic ecosystems when there is a shift in the natural sensory environment, frequently due to anthropogenic effects. The consequences associated with changes to the sensory environment of aquatic habitats can impact direct interactions between species. This, in turn, can lead to cascading changes in species community composition.

Given that human impacts, such as increased turbidity, can change aspects of the sensory environment, the initiation of activities or projects affecting aquatic environments must consider the broader scope of possible repercussions to the ecosystem and community structure. Anthropogenic activities often impact aquatic ecosystems by changing natural turbidity (Scheffer et al. 2001; de Jonge et al. 2002; Donohue and Molinos 2009; Gray et al. 2011). Many fish species are highly visual, relying on vision for prey detection, survival and mating cues (Guthrie and Muntz 1992; Domenici 2002; De Robertis et al. 2003; Jönsson et al. 2013). Therefore, it is crucial to study the effects of turbidity on multi-level scales to further the understanding of its far-reaching consequences and better enable the scientific community to assess the impacts of many everyday anthropogenic activities.

Towards this goal, the second chapter of this thesis reported on a laboratory experiment to examine the extent to which turbidity may give a sensory advantage to a species. I examined the visual detection of stimuli using a native predator-prey pair in multiple turbidity levels to determine whether either species gained a detection advantage. These experiments demonstrated that the prey species might gain an advantage over the predator within a range of turbidity, potentially impacting their relationship dynamics. These experiments were novel, in that many previous experiments that focused on the impact of turbidity on species did not remove other sensory cues (e.g., Miner and Stein 1996; Abrahams and Kattenfeld 1997; Carter et al. 2010). As such, these experiments limited both species to visual cues only and were effective in demonstrating how changes to a single abiotic characteristic can shift predator-prey dynamics. The natural environment consists of more than one predator-prey pair and contains multiple sensory cues. Therefore, if changes in turbidity can shift the dynamics of one predator-prey pair, do changes in turbidity impact the entire community?

This experiment prompted the meta-analysis, reported in chapter 3, that examined the magnitude of changes within fish communities associated with changes in turbidity. The meta-analysis evaluated whether changes to community composition at 13 dam sites were associated with an impoundment-induced change in turbidity. The creation of a reservoir provided a common factor associated with a change in turbidity, as it represents a known point in time when environmental conditions abruptly changed (Rosenberg et al. 1997). By using the date of impoundment, I could examine how species diversity metrics (biodiversity, species richness, and evenness) changed post-impoundment and test for

relationships with corresponding changes in turbidity. This meta-analysis examined shifts in the community as a whole in addition to subdividing the changes that occurred within the visually dependent and non-visually dependent species. This meta-analysis was unable to validate that the relationship between impoundment and turbidity can influence species diversity metrics, as it was probably constrained by the low number of studies with available turbidity data. Nonetheless, it succeeded in highlighting the relationship between increased turbidity and decreased biodiversity and evenness of the visual subset. The impact of increased turbidity on the majority of fish species has far-reaching implications for the broader aquatic community, including the potential for successful invasion of exotic species if environmental changes create a more favourable environment for the invasive species (Light 2003; Johnson et al. 2008; Abrahams et al. 2017).

Both of my studies revealed that turbidity decreases the ability of aquatic species to use available visual information and that these decreases may have far-reaching impacts. Changing the level of turbidity can influence the predator-prey dynamics of a native pair of species; additionally, the meta-analysis revealed reduced biodiversity in visually-dependent species associated with higher turbidity values. However, few studies have addressed anthropogenic impacts on the visual environment, as shown by the dearth of available turbidity information for reservoir sites in the meta-analysis. A decrease in the native species' abilities associated with changes in the sensory environment may create a window of opportunity for a non-native species that can utilize other sensory information to invade (Bergstrom and Mensinger 2009). Such invasions can significantly

alter ecosystems (Mack et al. 2000) by reducing native biodiversity when they become established (Leprieur et al. 2008). As such, these results point to a need for further study into the potential for invasion if anthropogenic activities may alter the sensory environment. My study demonstrated that changing the level of turbidity can influence detection rates within a given predator-prey pair and was associated with reduced biodiversity of visual species, a crucial next step in this field of research would be to determine whether increases in turbidity link to invasions by non-native species, thus wholly altering community structure.

This research expands our understanding of the importance of the sensory environment in species interactions and community composition. In the event that human activities alter the sensory environment, the consequences extend beyond just a few species; far-reaching impacts may cause cascading changes throughout the ecosystem. Turbidity alteration is happening worldwide as a result of farming, mining, urban development, human-educed eutrophication, and damming (Rosenberg et al. 1997; Scheffer et al. 2001; de Jonge et al. 2002; Donohue and Molinos 2009; Gray et al. 2011), supporting a need for further research into the links between changes in a sensory environment, community composition, and invasion of non-native species. Further research exploring potential shifts in advantages between native and invasive species using this experimental design would be beneficial. Using the methodology outlined in chapter 2, focussing solely on a change in the sensory environment that impacts a large portion of fish species, one can determine how such a change may impact natural

predator-prey relationships, as well as whether or not potential invaders are likely to succeed.

This study highlights a gap in current knowledge, by demonstrating significant changes to patterns in fish composition associated with a common anthropogenic change, impoundment of rivers, and a single change to the abiotic environment. This is of concern given the level at which anthropogenic activities have been impacting the abiotic environment of aquatic ecosystems for past decades. This thesis identified key interactions between turbidity levels and the biodiversity of visual fish species communities, emphasizing the need for further monitoring of turbidity and biodiversity in areas where dams are scheduled to be built or removed.

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Appendices

Appendix A: Location, sampling technique, and sampling year for pre and post-impoundment turbidity data. All turbidity data was measured in NTU.

Dam ID	Dam Name	Year Built	Pre-Impoundment				Post-Impoundment			
			Date	Location of Sampling	Sampling Technique	Source	Date	Location of Sampling	Sampling Technique	Source
1	John Day Dam	1968	1984	Upstream	Turbidimeter in field	Damkaer 1983	1994-95	In Reservoir	Turbidimeter in field	Gilbreath et al. 2000
2	Sanford Dam	1965	1983	Upstream	USGS Gauging station	Site 07227500, USGS	1987	In Reservoir	Turbidimeter in lab	Sullivan 1993
2	Ute Dam	1962	2002 and 2006	Upstream	Turbidimeter in field	New Mexico Lakes 2006	2002 and 2006	In Reservoir	Turbidimeter in field	New Mexico Lakes 2006
3	Petit-Saut Dam	1994-95	1995-96	Upstream	Turbidimeter in field	Merigoux and Ponton 1999	2002-03	In Reservoir	Turbidimeter in lab	Dominique et al. 2007

4	Salto Caxias Dam	1998	2006	Upstream	Turbidimeter in field	Behrend et al. 2012	2001	In Reservoir	Turbidimeter in field	Bini et al. 2008
5	Three Gorge Dam	2006	2002	In Reservoir (Prior to Impoundment)	MODIS Turbidity Data	Di Trapani et al. 2016	2006	In Reservoir	MODIS Turbidity Data	Di Trapani et al. 2016
6	Sulejowski Dam	1973	1965-70	In Reservoir (Prior to Impoundment)	Turbidimeter in field	Tomczak and Dominiak 2013	2003	In Reservoir	Turbidimeter in field	Tomczak and Dominiak 2013
7	Taylor Draw Dam	1984	1975	In Reservoir (Prior to Impoundment)	USGS Gauging station	Site 09306300, USGS	1987	In Reservoir	Turbidimeter in field	Tobin 1991
8	Canyon Dam	1964	1998	Upstream	In-Stream Turbidity Monitor	Guadalupe-Blanco River Authority 2016	2005-06	In Reservoir	In-Stream Turbidity Monitor	Guadalupe-Blanco River Authority 2016

9	Beaver Dam	1963	1979	Upstream	USGS Gauging station	Site 07048700, USGS	2001-03	In Reservoir	In-Stream Turbidity Monitor	Galloway and Green 2007
10	Grayrocks Dam	1980	1980	Upstream	USGS Gauging station	Site 0660100, USGS	2017	In Reservoir	Turbidimeter in field	Platte Alliance Water Supply 2019
11	Lostock Dam	1971	1994-95	Paired River	Turbidimeter in field	NSW Office of Environment and Heritage 2006	2008	In Reservoir	Turbidimeter in field	Dowling et al. 2010
11	Chichester Dam	1926	1994-95	Paired Rive	Turbidimeter in field	NSW Office of Environment and Heritage 2006	1994-95	In Reservoir	Turbidimeter in field	NSW Office of Environment and Heritage 2006

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Appendix B: List of studies used in this meta-analysis

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Appendix C: Technique, effort and timing of sampling for fish community abundance data pre- and post-impoundment.

	Pre-Impoundment			**Post-Impoundment**		
Dam Name	**Sampling Technique**	**Sampling Effort**	**Sampling Time**	**Sampling Technique**	**Sampling Effort**	**Sampling Time**
John Day Dam	Beach Seines at night	Monthly Collections	May-August 1984 and 1985	Beach Seines at night	Monthly Collections	May-August 1995
Sanford Dam	Seines	Monthly with 1-3 occasions per site	1954-55	Seines	Monthly 30-45 minute sampling times	September 1995-January 1996
Ute Dam	Seines	Monthly with 1-3 occasions per site	1954-55	Seines	Monthly 30-45 minute sampling times	September 1995-January 1996

Petit-Saut Dam	Gillnets overnight	Monthly Sampling	June 1994-December 1995 (except July and September 94 and August and October 95)	Gillnets overnight	Every 2 months	March 2002 to July 2003 and November 2003
Salto Caxias	Gill Nets that were inspected at dawn, dusk, and over night	Monthly Sampling	March 1997 to February 1998	Gill Nets that were inspected at dawn, dusk, and over night	Quarterly Sampling	March 1999 to February 2000

Three Gorge Dam	Gill Nets inspected at 7 am after 24 hours	8-14 days of continuous sampling	September 2006	Gill Nets inspected at 7 am after 24 hours	8-14 days of continuous sampling	November 2006
Sulejowski Reservoir	Dip nets and Electrofishing from shore and boat	Monthly sampling	summer to early autumn of 1968 and 1969	Dip nets and Electrofishing from shore and boat	Monthly sampling	Summer to early autumn from 2003-2005
Taylor Draw Dam	Electrofishing and Seining	Monthly Sampling	June to October 1983	Electrofishing, drift nets, and Seining	Monthly Sampling	June to October 1990
Canyon Dam	Seining	Historical collections obtained from	1938-68	Electrofishing and Seining	Historical collections obtained from	1970-2006

		museum collections, agency reports, and published documents.			museum collections, agency reports, and published documents.	
Beaver Dam	Electrofishing and Seining	Subset of 10 sites from a collection in a broad geographic range	1962-63	Electrofishing and Seining	Monthly	Sept. and Nov 1995; Jan., March-April, and Oct 1996; Jan., March-April, June and Oct 1997
Grayrocks Dam	Electrofishing and Seining	Historic data gathered from	1960-79	Electrofishing and Seining	Historic data gathered by	1980-2001

		University of Wyoming (UW), Wyoming Game and Fish Department (WGFD)			UW, WGFD, and Montana State University	
Chichester Dam	Electrofishing	Monthly	2006-2007	Electrofishing	Monthly	2006-2007
Lostock Dam	Electrofishing	Monthly	2006-2007	Electrofishing	Monthly	2006-2007